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Effect of Humidity on Photosynthesis and Water Relations of White Spruce Seedlings.

BY

Beverly Jane Marsden ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF FOREST SCIENCE

Edmonton, Alberta
Spring 1995

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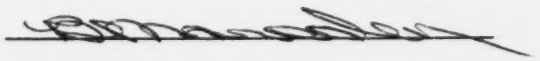

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommended to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled the Effect of Humidity on Photosynthesis and Water Relations of White Spruce Seedlings submitted by Beverly Jane Marsden in partial fulfillment of the requirements for the degree of Master of Science.

Dr. V. J. Lieffers, co-supervisor

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January 31, 1995

Abstract

The Effect of Humidity on Photosynthesis and Water Relations of White Spruce Seedlings During the Early Establishment Phase

The effect of a range of humidity levels on photosynthesis and water status of white spruce was investigated by subjecting three year old seedlings to three humidity treatments and two water stress treatments in controlled growth chambers set at 25, 50, and 80% relative humidity. Stomatal conductance and photosynthesis were substantially higher under 80% humidity than under 25 or 50% humidity, particularly for stressed seedlings. Increasing the humidity around the seedling improved water balance and alleviated water stress.

A study of varying aspen canopies on humidity levels in the field found that the absolute humidity difference between leaf and air under the partial and full canopies was lower than the clearcut. The young aspen stand provided adequate microsite conditions for white spruce seedlings. Silvicultural treatments which promote higher humidity levels on plantation sites should improve white spruce seedling performance during the early establishment phase.

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General Introduction

Successful plantation establishment of white spruce (*Picea glauca* (Moench) Voss) is a major silvicultural challenge in the boreal mixedwoods. There have been a number of decades of poor or inconsistent management of white spruce in these stands (Navratil et al. 1991), with 30% of the reforested sites in Alberta and 40-60% of the sites in Ontario falling below required stocking standards (Drew 1988; Margolis and Brand 1990). A re-evaluation of current silvicultural management of the mixedwoods, particularly in light of our increased understanding of forest ecosystems, is needed (Lieffers and Beck 1994). In natural mixedwood stands, white spruce and aspen are more productive than either species by itself (Lieffers and Beck 1994).

In the boreal mixedwood, white spruce occurs in association with aspen (*Populus tremuloides* Michx) or birch (*Betula* spp.) and regenerates in the understory (Brand and Penner 1990). White spruce is a shade tolerant species, and can attain maximum growth in 45% of full light (De Long 1991; K. J. Greenway unpublished). Understory conditions are less variable than clearcuts, and have higher levels of humidity, more shade, reduced wind speed, and lower incidence of frost (Johnson and Gorman 1977; Margolis and Brand 1990). These contribute to an improved water status in seedlings and a reduced susceptibility to dehydration (Childs and Flint 1987). Some problems with plantation performance can be attributed to the natural ecology of the species and the successional patterns of the planting site (Brand and Penner 1990).

The growth and survival of white spruce seedlings depends on their ability to adapt to environmental conditions (Burdett 1990). Plants which regenerate in forest understories, in small openings, or following minor disturbance have adapted to this form of regeneration through efficient resource use, slow initial growth, and great longevitiy (Margolis and Brand 1990). Clearcut environments are not the same as those in the understory or small forest openings, and as a regeneration niche are less than ideal. Evaporative demands can be severe on clearcut sites, since there is little surrounding vegetation or other structures to create shade or to reduce wind speeds, and this can create long term conditions of water stress (Burdett 1990). Clearcut sites are also susceptible to extremes of temperature and light, and to spring frosts, all of which can contribute to poor performance in white spruce (Mullin 1963).

Grossnickle (1988) reported that during the first 20 days following planting on a clearcut site, white spruce seedlings had very low rates of stomatal conductance. Xylem water potentials fell to between -2.5 and -3.0 MPa, below the turgor loss point, even though soil moisture levels were high. A similar study with container grown black spruce seedlings reported reduced growth, low mid-day stomatal conductance, and decreased mid-day water potential for at least 2 growing seasons when compared with natural seedlings (Bernier 1993). This indicates that the seedlings were initially unable to absorb enough water to function, and were unable to recover from this during the first month following planting.

Plantation failure has been attributed mainly to water stress, and to vegetative competition from shade intolerant weed species (Burdett 1990; Lieffers and Stadt 1994).

During early establishment, water stress results in either the immediate death of the seedling, or a delay in shoot growth, known as planting check, that puts the seedling at a competitive disadvantage with the surrounding vegetation (Margolis and Brand 1990). Water stress is a major cause of planting check, and can have a great impact on spruce establishment and survival (Burdett et. al 1984). Water stress occurs as a result of poor root to soil contact following planting, which limits a seedling's ability to absorb sufficient water to meet transpirational water losses (Grossnickle 1988; Grossnickel and Hiekurinen 1989; Burdett 1990).

Atmospheric humidity levels surrounding a seedling can partially determine the rate of transpirational water loss, and may significantly alter the influence of soil moisture stress on seedling growth, particularly during early establishment. Studies have shown that there is a direct relationship between stomatal closure and increasing absolute humidity differences between the leaf and the air (Jarvis 1976; Grossnickle and Blake 1986). White spruce stomata are particularly sensitive to low humidity levels, and this sensitivity is increased if the plant is experiencing water stress (Jarvis 1976; Grossnickle and Blake 1985). The closing of the stomata is the seedling's primary means of control over water loss at the leaf surface, but results in a reduction in photosynthesis (Hinckley et al. 1978; Margolis and Brand 1990; Burdett 1990).

Many studies focus on the development of new roots as a means of re-establishing root to soil contact and reducing the potential for drought stress. The ability of the seedling to produce new roots is influenced by cold storage, seedling water status and physiological condition, and by seasonal changes in shoot growth limiting the amount of

photoassimilates available for root growth (Burdett 1990). The environmental conditions on the planting site also affect root growth. Grossnickle and Blake (1985) found that root growth was reduced under low soil temperatures and under conditions of water stress. The lack of root growth in cold soils reflects a decrease in the metabolic activity of the plant (Grossnickle 1988).

While root development is crucial for the growth and survival of seedlings, there is some evidence to suggest that white spruce are physiologically incapable of rapidly producing new roots following transplanting. Grossnickel and Blake (1985) reported that the resistance to water flow through the roots was high following cold storage, and gradually decreased over 18 days, and suggested that the roots became more permeable as they acclimated to cool soil temperatures. Increased permeability of the root cell membranes would result in lower resistance to water flow. "Planting of cold stored seedlings into low soil temperatures may fail because of initially higher resistance to water flow through the roots" (Grossnickle and Blake 1985).

Since low soil temperatures are common in the boreal region, seedlings must be able to adapt to them. Van Den Driessche (1991) found that nursery pre-treatment of low (13°C) temperatures around the seedlings before lifting and storage greatly increased root growth capacity over seedlings grown at higher temperatures, but that this was only evident over the entire growing season. Possibly cooler nursery temperatures pre-condition the seedlings to cool spring temperatures, and speed up the process of acclimation.

The cycle of root growth is also important to the timing of lifting in spring and fall, and to the timing of planting, yet little is known about root growth in white spruce seedlings. Johnson-Flanagan and Owens (1985) found that roots of year old white spruce became dormant in winter and resumed growth in the spring before bud burst and shoot elongation. Planting in spring when air temperatures are warm enough to induce bud flush may direct stored and current photoassimilates to the growth of the new leaves and away from renewed growth of the roots. The cycle of root growth should be studied further in order to determine the optimum timing for new root regeneration following transplanting. Reducing the evaporative demand on the seedling may encourage rapid root growth, improve seedling physiology, and may affect plant metabolism under adverse soil temperatures. A reduced evaporative demand may also be important in reducing water stress prior to root re-establishment.

Studies on the timing of bud break in seedlings have focused on many environmental factors such as air temperature, light, soil temperature, soil moisture, and nutrient conditions (Lavender 1980). However, there is little data on the physiology of white spruce or the "environment most favourable for development between bud set and bud burst" (Ford 1980). Early bud flush may be caused by an increased number of leaf primordia in the resting bud (Lieffers 1987). High humidity may encourage early bud break by reducing the evaporative demand on the foliage, or by increasing the number of leaf primordia. Long term conditions of high humidity may improve survival and growth in white spruce seedlings.

An important factor in the annual height increment of seedling shoots is free growth following bud flush (Macey and Arnott 1986). In black spruce seedlings, the predetermined foliage in the bud can be supplemented up to 37% by free growth. The annual height growth is influenced by the ability of the shoot to renew and continue free growth after spring flush (Macey and Arnott 1986). If high humidity improves net photosynthesis, then it may also improve a seedling's ability for free growth following transplanting.

In this thesis, the effect of humidity on the physiology and water relations of white spruce was investigated under controlled environmental conditions. The effect of humidity on the ability of newly planted seedlings to resist water stress was examined by subjecting half the experimental group to drought stress. The objectives of this experiment were to determine the effect of a range of humidity levels on white spruce physiology, particularly in terms of stomatal conductance and photosynthesis, and to determine if a reduced evaporative demand on the foliage would have an impact on the seedling's ability to function under water stress.

The purpose of the field study was to determine the impact of a short canopy of aspen on relative humidity levels surrounding the seedling, and to determine if a young aspen stand would provide suitable conditions for white spruce seedling growth. The hypothesis that clearcutting reduces the humidity level around the seedling was also tested. Microsite conditions of soil temperature, soil moisture, absolute humidity difference between the leaf and air, and photosynthetically active radiation levels at seedling height were examined in a seven year old aspen stand regenerating from a clearcut. The

treatments were the uncut aspen, plots with half the aspen removed, and clearcuts. White spruce seedlings were planted to determine the effect of each treatment on seedling physiological parameters and water relations.

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Chapter 1

Effect of Humidity on the Photosynthesis and Water Relations of White Spruce Seedlings

Introduction

Water stress is the leading cause of poor growth and survival in transplanted white spruce seedlings (Burdett et al. 1984). The evaporative demand on a seedling affects the rate of transpiration water loss through the stomata. Several studies have shown that there is a direct relationship between stomatal closure and increasing absolute humidity difference (AHD), particularly when the plant is experiencing water stress (Jarvis 1976; Grossnickle and Blake 1985; Grossnickle and Blake 1986). The closing of the stomata is the plant's primary means of control over water loss at the leaf surface (Hinckley et al. 1978; Margolis and Brand 1990; Burdett 1990). There is strong evidence that low humidity directly affects stomatal conductance by lowering the water potential in the guard cells, causing loss of turgor in the guard cells and stomatal closure, before there is any loss in bulk leaf water potentials (Kaufmann 1976; Sandford and Jarvis 1986). This mechanism is particularly important for plants undergoing water stress. Kaufmann (1976) found that for absolute humidity differences above 6 $\mu g\ cm^{-3}$, stomata were nearly closed at xylem water potentials below -1.5 MPa. If the difference in absolute humidity between the leaf and the air were reduced, then the driving force for transpiration will be reduced,

and the stomata should remain open allowing photosynthesis to continue with a minimum of transpirational water loss. During early establishment, water stress on transplanted seedlings could be reduced by lowering the evaporative demand at the planting site.

Increased humidity is of particular importance for white spruce seedlings which are transplanted following cold storage. Grossnickle and Blake (1985) reported that the ability of mature foliage of white spruce to fully close the stomata is impaired by cold storage. This would contribute to water stress in the field, and is likely a factor in seedling survival. A high humidity level around a seedling would reduce the potential for dehydration at this stage by reducing the amount of water lost through these open stomata, and may alleviate the extent and duration of water stress following initial planting and during drought conditions.

Methods of promoting rapid root growth to re-establish root to soil contact have been suggested as a means of reducing water stress on seedlings. However, transplanting often causes a delay in the normal flush period of root activity that coincides with bud flush, and root activity is not fully resumed until the summer (Mullin 1963). Low soil temperatures in the spring reduce both the metabolic activity and the permeability of the roots, which require up to 20 days to acclimate following transplanting (Grossnickle and Blake 1987; Grossnickle and Heikurinen 1989). Another method of reducing water stress may be to reduce the evaporative demand on the foliage of the seedling. This would reduce seedling water losses to transpiration following transplanting, and before the root system can re-establish contact with the soil. If increased humidity levels promote better

seedling physiology and water status, then rates of root growth, bud flush, and annual height growth should also be improved.

In this study, the effect of humidity on photosynthesis and water status of white spruce seedlings was investigated under controlled growth chamber conditions. The effect of humidity on the ability of the newly planted seedling to resist water stress was examined by subjecting half the experimental group to drought stress. The purpose of the experiments was to determine if high humidity increases rates of stomatal conductance and photosynthesis in seedlings, and if high humidity improves the seedling's ability to function when it is experiencing drought stress. High humidity levels should improve the seedling's water balance by reducing the evaporative demand on the foliage. This may result in increased production of new roots, less negative root water potentials, and a more rapid time to bud flush.

Methods

Three Conviron CMP 3244 growth chambers were set at 25, 50, and 80% relative humidity (RH) levels. All were maintained at 22°C day/18°C night temperature, with photosynthetically active radiation (PAR) levels set at a minimum average PAR=290 μmol $m^{-2}s^{-1}$ for 18 hours per day. The light levels were tested with a Li-Cor Quantum/ Radiometer/Photometer Model Li-185 and a Lambda Instrument Corp. quantum sensor placed on the bench. The amount of PAR reaching the bench is the minimum amount of

light the seedlings will receive during the experiment, since light levels in a growth chamber decrease with distance from the light source (Zwiazek, pers. comm. 1995). Humidity levels were tested with a Bendix Psychron Model 566 hydrometer, and were found to be within 2% of the humidity levels recorded by the Conviron CMP 3244. The experimental parameters consisted of three humidity treatments, with two stress treatments (drought stressed and unstressed) under each humidity treatment. The experiment was replicated, with the first run from January 23 to February 14, 1994, and the second run from April 30 to May 10, 1994. It was necessary to use the same chambers for each designated humidity level in both experiments, since modification to the ventilation system was required to achieve the 25% humidity level.

Experiment 1

Three year old bareroot white spruce seedlings were obtained from Pine Ridge Provincial Forest Nursery at Smoky Lake, Alberta. The seedlings were 1.5 + 1.5 fall-lifted from a Whitecourt seed source (DS 70-18-5 83 SW). This means that the seedlings were grown for the first year and a half in the nursery before being transplanted outside for another year and a half, and then lifted in the fall and stored overwinter in a cooler at -2°C. After removal from cold storage, the seedlings were thawed at 4° C for 3 days prior to planting. For each of the six treatments, 49 seedlings were planted, which provided 7 seedlings for each stress level under each humidity treatment, over 7 measurement days,

for a total of 294 seedlings. Seedlings initially averaged 25.4 cm in height; 6 mm in root collar diameter; 6.7 g in shoot weight; and 1.56 g in root weight .

In order to simulate drought conditions for the water stress treatment, at the beginning of the experiment one half of the soil (Terra-Lite 2000 Metro-Mix 290) was mixed with water until it reached a water content of 10% per volume. The remaining soil was mixed with 20% water per volume, and constituted the unstressed treatment. This was tested prior to the experiment using a Trase Systems TDR (Soilmoisture Equipment Corp.) which incorporates the "principle of Time Domain Reflectometry in order to convert the travel time of a high-frequency, electromagnetic pulse into volumetric water content". The seedlings were planted in 155 mm standard pots, and labeled. Half the seedlings began in wet soil and were watered every second day. The seedlings for the stressed treatment began in the dryer soil, and were watered when shoot xylem water potentials reached approximately -2.0 MPa (Day 10). The shoot xylem water potentials of the stressed plants were averaged on each measurement day to assess when the seedlings were approaching -2.0 Mpa. The stressed and unstressed seedlings were alternately placed within each chamber, and rotated around the chamber every second day.

A preliminary experiment was conducted to determine a method of maintaining similar soil moisture levels among humidity treatments. White spruce seedlings were planted in 155 mm pots. Granite gravel, perlite, and plastic mulches were tested by covering the soil with each material. A control group of plants with uncovered soil was also included in the experiment. The plants were divided into two groups, with one group placed in a humid greenhouse at 55% relative humidity, and the other group put into a

growth chamber set at 30% humidity. All the plants were initially well watered, and then left to dry for 20 days, with the pot weights measured every second day. Granite gravel proved to be the most effective at maintaining similar soil moisture conditions between the three humidity treatments. Thus a 4 cm layer of granite gravel was placed over the soil of all the 25% humidity treatment seedlings.

On day 11, all the plants were fertilized with a 20-20-20 fertilizer (0.25 grams per litre of water) at a rate of 100 ml per plant. Fertilizer was added 24 hours after watering. All experimental measurements were taken on days 3, 6, 9, 11, 17, 21, and 25 after planting.

An LCA-2 Infrared Gas Analyzer (IRGA) equipped with a conifer cuvette was used to measure net assimilation, transpiration, and stomatal conductance to CO_2. Air flow rate was set at 8 ml/s, and a quartz halogen lamp was positioned to boost light to 1000 $\mu mol\ m^{-2}s^{-1}$. A high speed fan built into the cuvette created turbulence, reducing the boundary layer resistance around the leaves. Ambient air was drawn in from a 4 m high tower positioned outside the growth chambers, and passed through a silica gel desiccant (anhydrous $CaSO_4$, 6 to 16 mesh) before entering the cuvette. The measurements were conducted inside the chamber, so that the seedlings were not exposed to higher or lower humidity levels during measurements. Half the plants in each chamber were measured in the morning, and the remaining half in the afternoon, with measurements alternating between stressed and unstressed seedlings.

A lateral branch mid-way along the seedling was selected for gas exchange measurements. To lessen the variability of the measurements, attempts were made to

select branches uniform in size and position on the seedlings. The leaves were stripped from the branch at point of contact with the cuvette to ensure a better seal. Care was taken to avoid tearing the outer bark of the branch. After measurement, the branch was clipped and sealed in a plastic bag for leaf area analysis. The air temperature inside the cuvette was used as an estimate of leaf temperature for the gas exchange measurements. The value for boundary layer resistance was from a previous study on three year old black spruce seedlings (S.E. Macdonald, pers. comm. 1993). The atmospheric pressure was obtained from Environment Canada's Climate Services, as recorded at noon on each measurement day at the Edmonton Municipal station. In the lab, the branch used for IRGA analysis was dipped in liquid nitrogen for 10 seconds to ease the removal of the leaves. The leaf area of each sample was then determined with a LI 3100 Leaf Area Meter (Lambda Instruments Corp.). Three measurements of the projected leaf area were taken and averaged, then multiplied by 2 to provide the total estimated leaf area. All recorded measurements from the IRGA were run through a series of calculations to obtain the gas exchange parameters (von Caemmerer and Farquhar 1981).

The leaf temperature was measured using a thermocouple junction with copper-constantan wire 0.12 mm in diameter formed into a 3 mm loop. The loop was slipped over the leaf and twisted slightly to improve wire contact with the leaf. An ice-point junction attached to a multimeter provided a voltage reading which was then multiplied by 25.2 to calculate leaf temperature. This was recorded for five leaves per plant and averaged. The evaporative demand on the seedling is the absolute humidity difference (AHD) between the needle and the air, and was calculated for each chamber using air

temperature, needle temperature, and relative humidity around the seedling. The following formulas were used to calculate absolute humidity difference:

$$\ln e_s = 21.832 - (5.3475 \times 10^3 / \text{Temp K°})$$

$$e = (RH/100) \times e_s$$

$$Pv = 217 \times e / \text{Temp K°}$$

$$VPD = e_s - e$$

$$AHD = Pv\ (\text{leaf}) - Pv\ (\text{air})$$

where e_s is the saturation vapour pressure (kPa), e is vapour pressure (kPa), RH is the relative humidity (%), Pv is the absolute humidity ($\mu g\ cm^{-3}$), VPD is the vapour pressure deficit (kPa), and AHD is the absolute humidity difference (Lee 1978).

After gas exchange measurements were completed, each plant was cut just above the root collar and the outer bark stripped off. The shoot was pushed gently into a Scholander pressure bomb (PMS Instrument Company, US), with the cut end projecting through the rubber stopper. Compressed nitrogen gas was released gradually into the chamber increasing the pressure, and a reading was taken when the xylem sap appeared on the cut surface of the stem. This pressure reading is a good estimate of shoot xylem water potential in the plant (Ritchie and Hinckley 1975).

Each sampled plant was examined for the number of new white roots it had produced. On days 3 and 6, the number of new white roots under 10 mm in length was counted. Also on day 6 and for the remaining measurement days, the number of white roots longer than 10 mm was recorded. For days 9 to 25, the water potentials were determined for the new white root tips of sampled plants from the 25% and the 80% chambers. Time constraints inherent in the method prevented the examination of the

plants under the 50% humidity treatment. The root tips of the seedlings were clipped for water potential analysis in a Triple Hygrometer (Plant Water Status Instruments, Inc.) and an SC-10A Thermocouple Psychrometer equipped with an NT-3 Nanovoltmeter Thermometer (Decagon Devices Inc.). For each plant, two white root tip samples were taken and placed into two separate psychrometer chambers. The chambers were sealed for one hour to allow the sample to equilibriate, and microvolt and temperature readings were taken (Joly 1985; Spanner 1951).

On each measurement day, the soil from the pot of each sampled plant was collected in a plastic bag, weighed, and dried for 24 hours at 105°C. The dry soil was weighed, and soil moisture content expressed on a dry-weight basis.

The rate of bud flush of the terminal bud, the top three lateral buds, and the percent bud flush for the whole seedling was recorded for all remaining plants every second day from the beginning of bud flush. The percentage bud flush was determined by counting the number of flushed buds from the total number of buds. Due to time constraints, data were not collected for the 50% humidity treatment groups.

Experiment 2

Experiment 2 was conducted in the same growth chambers and maintained under the same environmental conditions. The following changes were made to the method for the second run. The seedlings were obtained from Pine Ridge Provincial Forest Nursery at Smoky Lake, Alberta. The seedlings were Plug + 1.5 fall '93 lifted (DP 88-12-6-82

SW). This means that the seedlings were grown for the first year and a half in plug containers in the nursery before being transplanted outside for another year and a half, and then lifted in the fall and stored overwinter in a cooler at -2°C. After removal from cold storage, the seedlings were thawed at 4° C for 3 days prior to planting. Seedlings initially averaged 31.5 cm in height; 6.6 mm in root collar diameter; 17.6 g in shoot weight; and 19.1 g in root weight. The shoot and root weights of these seedlings were considerably larger than those used in Experiment 1. The stressed group needed to be watered twice, on days 5 and 13, since shoot xylem water potentials were approaching -2.0 MPa. From results of the first experiment, we determined that it was necessary to add granite gravel to the stressed group under the 50% humidity treatment to reduce evaporation from the soil.

Photosynthetic measurements are usually taken with the air going into the cuvette dried as much as possible, so that the humidity of the air is constant for each plant. Ambient humidity consists of the humidity level in the chamber plus the humidity provided by transpiration of the plants in the chamber. The humidity in the cuvette consists of the humidity level of the air going into the cuvette plus the transpiration humidity provided by the enclosed branch. Adjusting the RH_{out} of the cuvette to the humidity level set for the chamber created a humidity condition in the cuvette similar to that within the chamber. In the 25% humidity chamber, the air was drawn through a 4 m tower outside the chamber and passed through two drying chambers filled with a silica gel desiccant of anhydrous $CaSO_4$. The by-pass valve was adjusted to maintain RH_{out} at 25%. For the 50% treatment, the left drying chamber was emptied of silica gel desiccant, and the by-pass valve was opened to produce an RH of 50% in the cuvette during photosynthesis

measurements. For the 80% chamber, the air drawn in from the tower was first passed through a 2000 mL filter flask half filled with water. The hose from the tower was connected to the flask through a rubber stopper, and attached to an airstone in the flask, so that the air was first bubbled through water to increase its humidity (Johnson and Ferrell 1983). Another connecting hose was attached to the flask's side arm, and then to the IRGA. The left drying chamber was emptied of silica gel desiccant, and the by-pass valve adjusted to maintain RH_{out} at approximately 80% humidity.

The number of new white roots longer than 10 mm was counted for each plant sampled on days 8, 10, and 12 of the experiment. Due to time constraints, the root water potentials were not measured.

On day 6 of the experiment, fertilizer was added to the seedlings in the same quantity as in Experiment 1. Measurements were taken on days 4, 6, 8, 10, 12, and 14 after planting.

To investigate leader growth and new leaf development, the last group of seedlings was allowed to fully flush and set buds. The water potentials measured on day 14 were taken using a lateral branch instead of the entire seedling. The growth chamber conditions were maintained as before. The remaining 21 unstressed plants were watered every second day while the remaining 21 stressed plants were watered every sixth day. On days 35 and 50, the seedlings were sprayed with Pirimor 50 WP (pirimicarb) at the rate of 0.5 grams per litre of water, to control aphids. The seedlings were fertilized again on day 38 with 1.2 grams per litre of water of 35-5-10 with trace elements (Fe, Cu, Mn, Zn, and $MgSO_4$) at the rate of 150 ml per plant. On day 96 the seedlings were harvested, and the

leaders clipped and placed in plastic bags. The soil was collected for gravimetric measurement of moisture content, as before. In the lab, the leaders were dipped in liquid nitrogen for 10 seconds to ease the removal of leaves. A sample of 10 needles per leader was taken and the lengths of each needle recorded. The widths of the sample needles were measured using a 10/.40 microscope (Wild Leitz Canada Ltd.) equipped with an internal optical scale. The total number of leaves per leader were counted, and the total number of leaves divided against the leader length to calculate the leaf internodal length of the leaders.

The rate of flushing of the top three lateral buds and the terminal bud was recorded. Due to time constraints, the percentage of flushing was estimated visually for the whole seedling. Three sample branches at mid-seedling height were ranked between 1 and 4, representing 25, 50, 75, or 100% of buds flushed on each branch. This was used to estimate total bud flush for each seedling. Bud flush was recorded every second day from the beginning of bud flush.

Statistical Analysis

Analyses of variance were performed using the general linear model (two way ANOVA with interaction, mixed model). Where significant differences occurred, the contrast testing procedure of SAS (SAS Institute Inc) was used to test for these differences. The significance level of each comparison test was adjusted to $\alpha' = 0.0127$ for an experiment-wise error rate of $\alpha = 0.05$, according to the Dunn-Sidak method for

non-orthogonal planned comparisons (Sokal and Rohlf 1981). The rate of overall bud flush was tested using repeated measures analysis of variance. The rates of bud flush of the terminal and top three lateral buds were tested using the general linear model ANOVA for a day mid-way between the beginning and end of flushing. Graphing was done using the Means procedure of SAS, incorporated into Sigma Plot (Jandel Scientific Inc.).

Results

In the first experiment, the absolute humidity difference (AHD) for each chamber averaged 22.69 (±1.05), 17.81 (±0.64), and 7.59 (±0.68) μg H_2O cm^{-3} for the 25, 50, and 80% humidity treatments, respectively. The relative humidity (RH) in the 50 and 80% chambers averaged 43% and 79%, respectively, during the course of the experiment. The humidity in the 25% chamber fluctuated between 25% and 35% RH during the first week. By day 9, improvements to the ventilation system reduced the humidity to approximately 25% for the remainder of the experiment. Overall, the humidity in the lower chamber averaged 29% RH.

In Experiment 2, the absolute humidity difference for each chamber averaged 20.95 (±0.56), 16.50 (±0.23), and 6.82 (±0.50) μg H_2O cm^{-3}, for the 25, 50, and 80% humidity treatments. The ventilation system could not adapt to the increased humidity in the air due to spring time conditions, so that the humidity level in the 25% chamber

averaged 31% RH. The remaining chambers averaged 51% and 80% over the course of the experiment.

For the IRGA measurements, the relative humidity going into the cuvette was increased from 7% for all treatments in the first experiment, to an average of 12%, 35% and 63% for the 25, 50, and 80% treatments, respectively. Relative humidity levels inside the cuvette averaged 28% (±3), 50% (±4), and 79% (±2), for the 25, 50, and 80% chambers, respectively.

Net Assimilation:

In Experiment 1, the unstressed seedlings had higher ($P<0.0001$) net assimilation rates under 80% humidity than under 25 or 50% humidity (Table I-1; Fig. I-1a). Net assimilation was also higher ($P<0.0001$) under 50% humidity as compared to 25% humidity (Table I-1; Fig. I-1a). Under 25% humidity, plants did not achieve net assimilation levels above 12 μmol $m^{-2}s^{-1}$, half that of the 80% treatment (Fig. I-1a). In the drought stressed treatment, there was no difference in net assimilation rates between the 25 and 50% humidity treatments, but at 80% humidity net assimilation rates were higher ($P<0.0001$) than for plants grown under 25% or 50% humidity levels (Table I-1; Fig. I-1f). Maximum net assimilation rates for the 80% stressed treatment were twice that of the other two stressed treatments (Fig. I-1f). In Experiment 2, net assimilation was higher ($P<0.0001$) under 80% humidity for both the stressed and the unstressed treatments (Table I-1; Figs. I-2a and I-2f), while differences in net assimilation between the 25% and

Table I-1: **Results of Analyses of Variance - Probability values for photosynthetic and water relations data.**

Source	Net Assimilation		Stomatal Conductance		Transpiration		Shoot Water Potential		Soil Moisture Content	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Stress	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Humidity	0.0001	0.0001	0.0001	0.0001	0.0001	0.0772	0.0001	0.0032	0.0001	0.0001
Day	0.0001	0.0029	0.0001	0.8847	0.0001	0.0017	0.0117	0.0001	0.0001	0.0001
Stress*Humidity	0.0035	0.1806	0.0001	0.0001	0.0250	0.0536	0.7028	0.2311	0.0001	0.0001
Stress*Day	0.0001	0.0001	0.0002	0.0019	0.0006	0.0001	0.0008	0.0020	0.0001	0.0001
Humidity*Day	0.0660	0.1737	0.0001	0.2739	0.0521	0.0010	0.0008	0.0148	0.0011	0.0178
Stress*Hum*Day	0.1970	0.0128	0.2870	0.0042	0.4757	0.1390	0.0005	0.6926	0.0025	0.1997
CONTRASTS										
Unstressed										
80% vs 50&25%	0.0001	0.0001	0.0001	0.0001	0.0001	0.3483	0.1455	0.0005	0.0001	0.0001
25% vs 50%	0.0001	0.1036	0.0107	0.8079	0.0003	0.0020	0.0056	0.8388	0.0006	0.0003
Stressed										
80% vs 50&25%	0.0001	0.0001	0.0001	0.0016	0.0001	0.5646	0.0248	0.2022	0.0043	0.0620
25% vs 50%	0.4115	0.0001	0.9438	0.6338	0.5662	0.9555	0.0002	0.5250	0.0013	0.1006

*Note: For Contrasts, the P value must be less than 0.0127 to be significant at $\alpha = 0.05$.

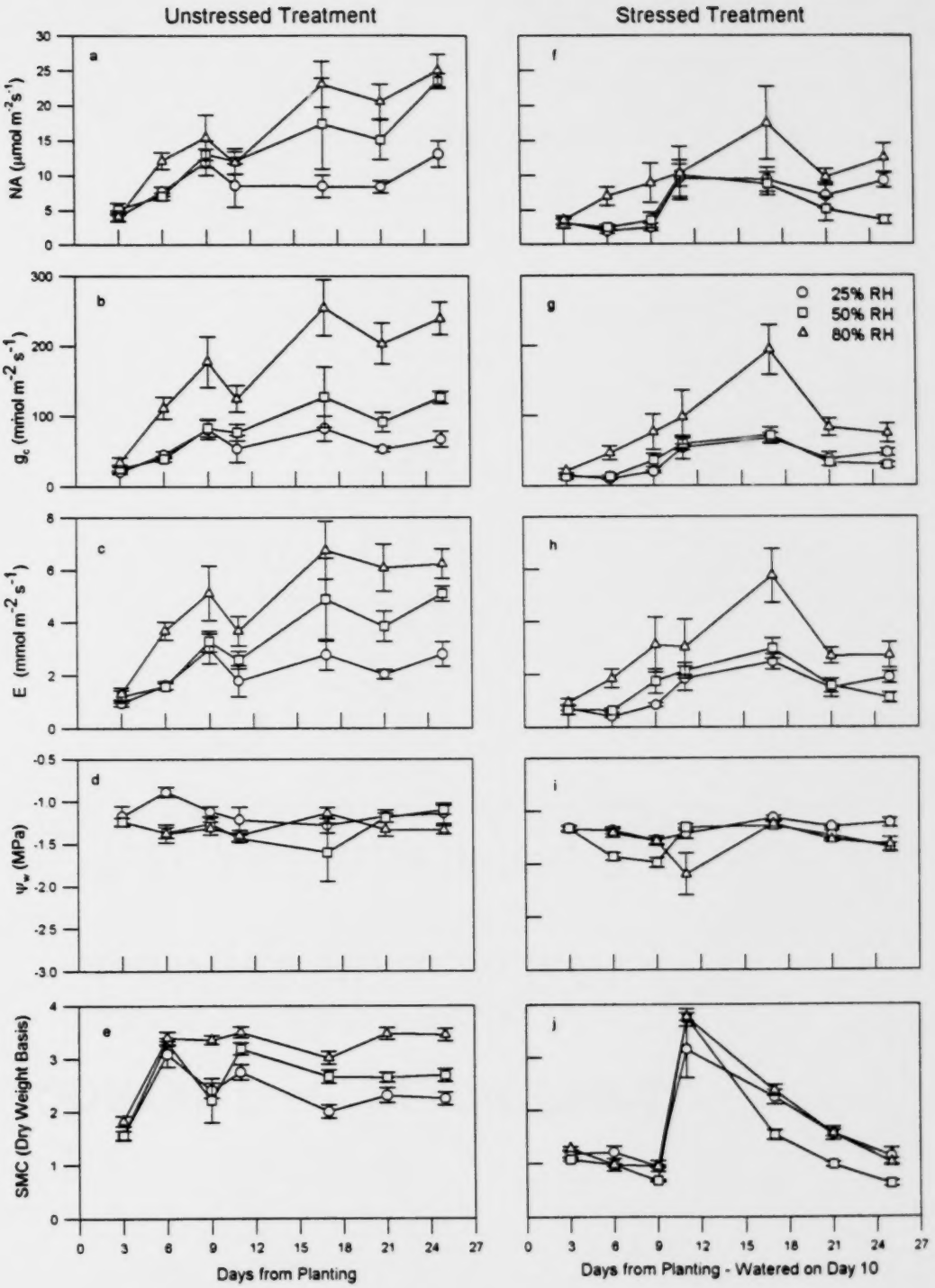

Figure I-1 (a to j). Effect of 25%, 50%, and 80% humidity on photosynthesis (NA), stomatal conductance (g_c), transpiration (E), xylem water potential (ψ_w), and soil moisture content (SMC) of unstressed and drought stressed white spruce seedlings in Experiment 1.

the 50% humidity treatments did not occur in unstressed plants. Under drought stress, net assimilation was higher ($P<0.0001$) at 50% humidity than at 25% humidity (Table I-1; Fig. I-2f).

Stomatal Conductance:

In Experiment 1, the stomatal conductance of unstressed seedlings was higher ($P<0.0001$) at 80% humidity than at either 25 or 50% humidity, and was also higher ($P<0.0107$) at 50% humidity than at 25% humidity (Table I-1; Fig. I-1b). Under drought stress, plants showed higher ($P<0.0001$) stomatal conductance under 80% humidity, but there were no differences between the 25 and the 50% treatments (Table I-1, Fig. I-1g).

Stomatal conductance in Experiment 2 followed a similar trend to that of Experiment 1. Stomatal conductance was higher at 80% humidity for both the well watered ($P<0.0001$) and the drought stressed ($P<0.0016$) seedlings (Table I-1; Figs. I-2b and I-2g). There was no difference in the stomatal conductance of plants under the 25 and the 50% humidity treatments (Table I-1). These seedlings showed very low stomatal conductance, and neither the unstressed nor the drought stressed plants achieved 100 mmol $m^{-2}s^{-1}$ during the course of the two experiments.

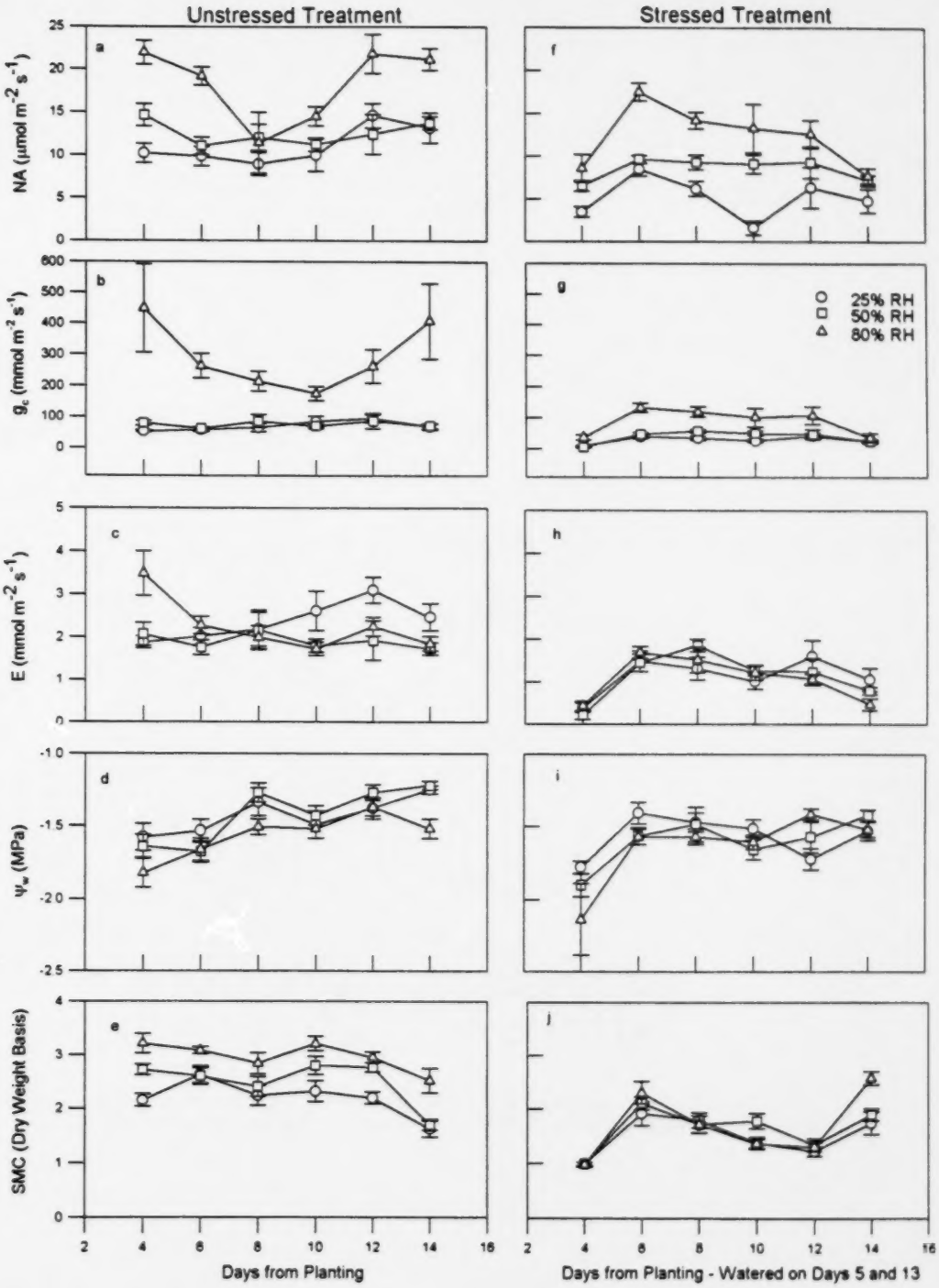

Figure I-2 (a to j). Effect of 25%, 50%, and 80% humidity on photosynthesis (NA), stomatal conductance (g_c), transpiration (E), xylem water potential (ψ_w), and soil moisture content (SMC) of unstressed and drought stressed white spruce seedlings in Experiment 2.

Transpiration:

In Experiment 1, the air entering the cuvette and the IRGA was dried to 7% relative humidity. Transpiration levels were higher ($P<0.0001$) under 80% humidity treatment for both the unstressed and the drought stressed treatments (Table I-1, Figs. I-1c and I-1h). The high calculated transpiration rates were an indication of the open condition of the stomata and the dry air of the cuvette, rather than a representation of actual transpiration levels under 80% humidity. For the well watered plants, transpiration levels under 50% humidity were also higher ($P<0.0003$) than those under 25% humidity (Table I-1; Fig. I-1c). For the drought stressed plants, there was no difference between transpiration levels at 25% and 50% humidity (Table I-1).

In Experiment 2, the RH_{out} was adjusted so that the humidity in the cuvette was similar to the humidity in each chamber. Among the well watered plants, transpiration was lower ($P<0.0020$) under 50% humidity than under 25% humidity, and this difference increased over time (Table I-1; Fig. I-2c). The plants under 80% humidity did not transpire at significantly different rates compared to seedlings from the 50% and 25% chamber (Table I-1). There were no significant differences in transpiration rates among the drought stressed treatments.

Shoot Xylem Water Potential:

In Experiment 1, humidity had an effect ($P<0.0001$) on shoot water potentials in both the well watered and the drought stressed treatments (Table I-1). For the well watered plants, shoot water potentials were lower ($P<0.0056$) under 50% humidity than under 25% humidity (Table I-1; Fig. I-1d). This trend was similar for drought stressed plants, with shoot water potentials being lower ($P<0.0002$) under 50% humidity than under 25% humidity (Table I-1; Fig. I-1i). This corresponds to the lower soil moisture levels in the 50% stressed treatment (Fig. I-1j). The interaction of humidity with stress level on shoot water potentials was not significant. For the other interaction terms, significant levels were due to the experimental design of changing soil water potential with time (Table I-1).

In Experiment 2, shoot water potentials for the unstressed group under 80% humidity were more negative ($P<0.0005$) than those under either 25 or 50% humidity treatments (Table I-1; Fig. I-2d). There was no difference between the 25 and the 50% treatments for the unstressed treatment. Among the drought stressed treatments there were no differences in shoot water potentials. After the initial watering on day 5, shoot water potentials remained constant throughout the experiment, and the seedlings were not stressed as much as in Experiment 1 (Figs. I-1i and I-2i).

Soil Moisture Content:

In Experiment 1, differences in soil moisture content occurred in both the unstressed and the drought stressed treatments (Figs. I-1e and I-1j). For well watered seedlings, there was a difference ($P<0.0006$) in soil moisture content between the 25 and 50% humidity treatments, and also a difference ($P<0.0001$) between these two treatments and the 80% humidity treatment (Table I-1). Soil moisture contents were similar between these treatments for the first six days, and then diverged, despite watering every second day. The 80% humidity treatment retained the most soil moisture, followed by the 50%, and then the 25% treatments (Fig. I-1e). The stressed treatments also showed differences ($P<0.0043$) in soil moisture content, with seedlings under 80% humidity having a higher soil moisture content than either the 25 or the 50% humidity treatments (Table I-1). Unlike the well watered seedlings, the drought stressed group under 50% humidity had substantially lower soil moisture contents ($P<0.0013$) than the 25% stressed treatment (Table I-1; Fig. I-1j).

The interaction terms of stress and humidity, stress and day, humidity and day, and stress with humidity by day were necessarily significant due to the design of the experiment. The soil moisture content was different ($P<0.0001$) between the stressed and unstressed treatments, and this difference changed ($P<0.0001$) during the course of the experiment, since the stressed treatments began with less soil moisture and were left to dry until shoot water potentials reached approximately -2.0 MPa, then were watered and left to dry again (Table I-1). Soil moisture content was affected ($P<0.0001$) by humidity

levels in each chamber, with the 80% treatment showing lower rates of soil water evaporation than the other two humidity treatments (Table I-1; Fig. I-1e). The interaction of humidity with day on soil moisture content was also significant ($P<0.0011$), since soil moisture declined with time in the stressed treatments due to experimental design (Table I-1).

In Experiment 2, the addition of granite gravel to the 50% stressed treatment improved control over soil moisture levels, so that there was no difference in soil moisture content between the stressed treatments under the three humidity treatments (Table I-1; Fig. I-2j). For the well watered treatments, the trend remained as in Experiment 1. A difference ($P<0.0003$) occurred between soil moisture contents under 25 and 50% humidity (Table I-1). The soil moisture content under 80% humidity was higher ($P<0.0001$) than under the 25 and 50% humidity treatments (Table I-1; Fig. I-2e). Again, differences for stress and day, and for the interaction between stress and day, humidity and day, and stress and humidity, were due to experimental design (Table I-1).

Number of New White Roots:

For days 3 and 6 in Experiment 1, the number of new white roots under 10 mm was not significantly different between the stress treatments and the humidity treatments (Table I-2). There was an increase in the number of new white roots from day 3 to day 6, as expected. For the number of new white roots greater than 10 mm, significant differences occurred for the variables stress and day, since there were two stress

Table I-2: **Result of Analyses of Variance: Probability values for root count and root water potential data.**

Source	Roots <10 mm Exp. 1	Root Count >10 mm Exp. 1	Exp. 2	Water Potential Exp. 1
Stress	0.4990	0.0001	0.0010	0.0001
Humidity	0.7641	0.7231	0.3925	0.9682
Day	0.0001	0.0001	0.0163	0.0979
Stress*Humidity	0.0842	0.0301	0.3346	0.0004
Stress*Day	0.5219	0.0182	0.1894	0.6002
Humidity*Day	0.9770	0.3704	0.1725	0.7996
Stress*Hum*Day	0.0243	0.5943	0.1906	0.2656

treatments, and since the number of new roots increased with length of time from planting. There was also an interaction ($P<0.0301$) between stress and humidity, with unstressed plants producing more white roots than stressed plants (Table I-3). The low number of new roots in the 50% stressed seedlings is likely due to the lower soil moisture content for this group. The interaction ($P<0.0182$) between stress and day is due to increased root production in unstressed plants over time. When unstressed and stressed treatments were separated for contrast testing between humidity levels, there were no significant differences in the number of new white roots developed under each humidity level (Table I-2).

In Experiment 2, the number of new white roots was not significantly different at any humidity or stress level (Table I-2). The interaction terms of stress and day were significantly different due to experimental design. Seedlings in Experiment 2 were considerably larger than those used in Experiment 1, and produced a greater number of new roots (Table I-3).

Root Water Potential:

In Experiment 1, there was a difference ($P<0.0001$) in root tip water potential between the stressed and unstressed seedlings, with stressed seedlings having lower values (Table I-2). There was also an interaction ($P<0.0004$) between humidity and stress on root water potentials (Table I-2). Root water potentials of unstressed seedlings were

Table I-3: **Mean values for number of new white roots > 10 mm produced under three humidity conditions and two stress levels, for measurement days 6 to 25 in Experiment 1, and days 8, 10, and 12 from planting in Experiment 2.**

Unstressed	**Exp. 1**	**Exp. 2**
25%	29.26 (±5.96)	40.90 (±4.74)
50%	37.40 (±6.92)	32.14 (±4.39)
80%	27.50 (±4.33)	30.67 (±5.02)
Stressed		
25%	18.90 (±3.92)	23.57 (±3.62)
50%	8.22 (±1.70)	22.33 (±2.94)
80%	14.57 (±2.86)	25.00 (±4.03)

higher for the 80% treatment than for the 25% treatment. This trend was reversed for the stressed seedlings. While plants under 25% humidity retained similar root water potentials between stressed and unstressed seedlings, there was a notable difference between seedlings under 80% humidity. The root water potentials for stressed plants at 80% humidity were considerably lower than the unstressed plants in this group (Table I-3, Figs. I-3a and I-3b). Average water potentials were fairly constant over the course of the experiment for stressed seedlings, with the 80% treatment maintaining potentials of -1.49 MPa, and the 25% treatment averaging -1.18 MPa. Water potentials of the roots did not fall below -2.0 MPa.

Leader Length and Morphology:

In Experiment 2, leaf morphology in terms of length and width was not affected by either stress or humidity. Leader length was also unaffected. Leaf internodal length was shorter ($P<0.0100$) at 80% humidity in unstressed seedlings (Table I-4). There was no difference in leaf internodal lengths among stressed seedlings (Table I-4, Fig. I-4). The sample size in the study of leader growth was small (42) and was reduced to 41 by the loss of a seedling.

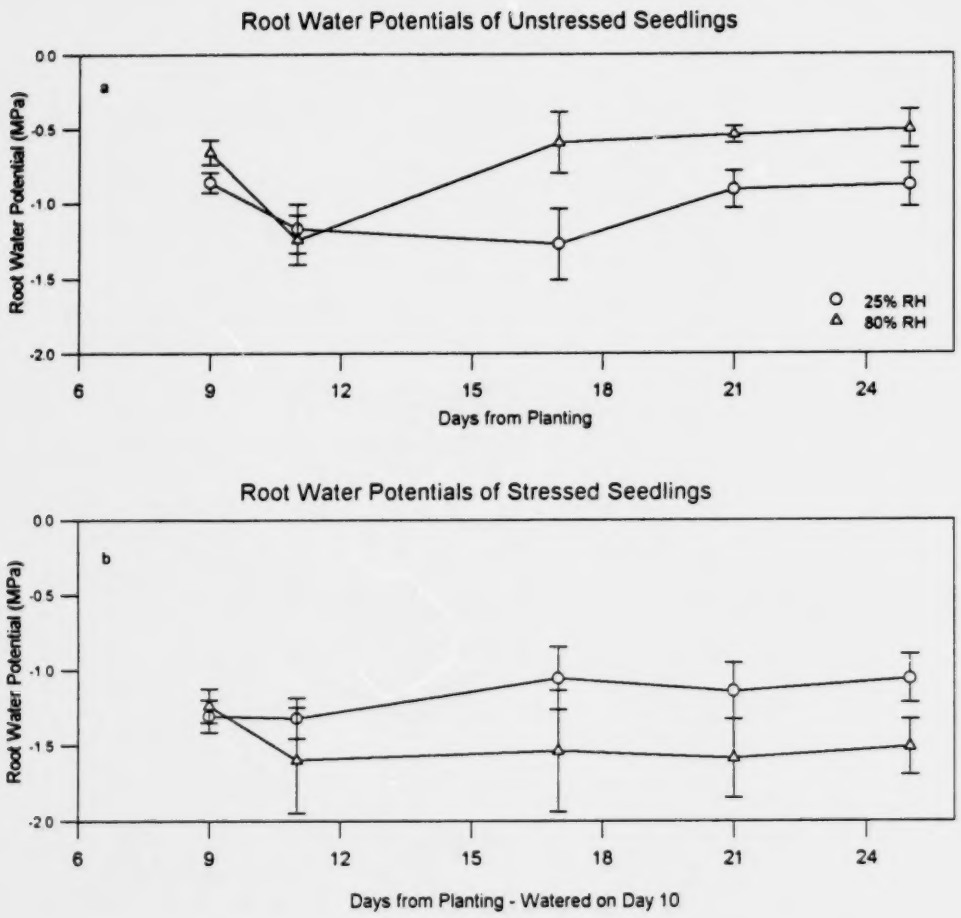

Fig. I-3 (a,b): Root water potentials for unstressed and stressed white spruce seedlings at 25% and at 80% humidity in Experiment 1.

Table I-4: **Probability values for leader length, leaf morphology, and leaf internodal length, for white spruce seedlings grown under three humidity levels for 96 days in Experiment 2.**

Source	Leader Length	Number of Leaves	Leaf Length	Leaf Width	Leaf Internodal Length
Stress	0.1473	0.9535	0.0676	0.3633	0.2039
Humidity	0.1726	0.7409	0.2759	0.4393	0.0159
Stress*Hum	0.7264	0.4102	0.0797	0.8081	0.1748
Contrasts					
Unstressed					
80% vs 25 & 50%	-	-	-	-	0.0100
25% vs 50%	-	-	-	-	0.2817
Stressed					
80% vs 25 & 50%	-	-	-	-	0.8088
25% vs 50%	-	-	-	-	0.0549

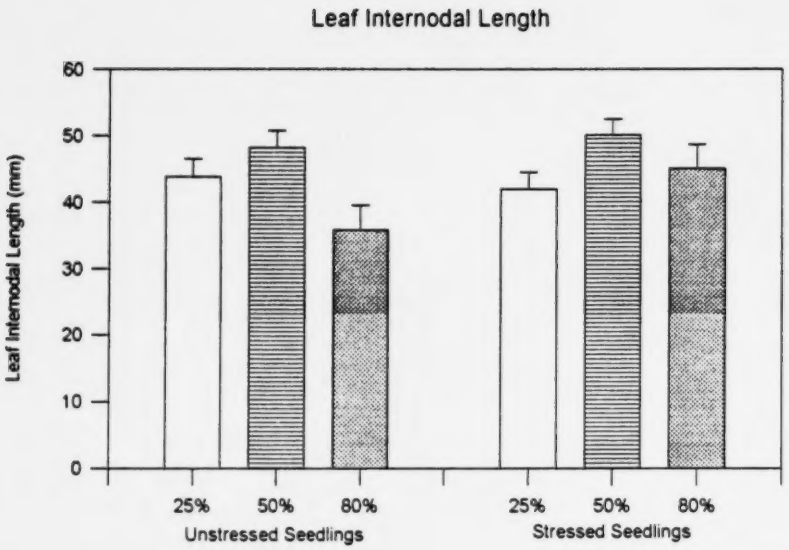

Fig. I-4 Leaf internodal length of the leading shoot of unstressed and stressed white spruce seedlings grown under different humidity levels for 96 days in Experiment 2.

Rates of Bud Flush:

In Experiment 1, bud flush was later in the 25% humidity level than the 80% ($P<0.0001$), and bud flush was later in the stressed treatment ($P<0.0075$) than the unstressed. There was no interaction between stress and humidity (Table I-5; Figs. I-5a and I-5d). Data were not available for the 50% humidity treatment group. Terminal bud flush for stressed and unstressed seedlings was analyzed on day 6, mid-way between the beginning and end of flush for the unstressed treatment. There were no significant differences in the effect of humidity or stress on terminal bud flush (Table I-5). The lateral bud flush was analyzed on day 8. Again there were no significant differences (Table I-5).

In Experiment 2, there was also a difference ($P<0.0001$) in overall bud flush between the three humidity treatments, and a difference ($P<0.0001$) between stress treatments, but there was no interaction between stress and humidity (Table I-5). Overall rates of bud flush were faster under 80% humidity than under either 25 or 50% humidity (Figs. I-6a and I-6d). Terminal bud flush was analyzed for day 10, and there was a difference ($P<0.0294$) between the seedlings under 80% humidity and those under 25 and 50% humidity (Table I-5). There was also a difference ($P<0.0128$) between the 25 and the 50% treatments (Table I-5). Stress had no significant effect on terminal bud flush, and there was no interaction between stress and humidity treatments. Terminal bud flush occurred faster at 80% humidity in both stressed and unstressed grouops (Figs. I-6b and I-6e). Lateral bud flush was analyzed on day 8, and differences were found for humidity ($P<0.0020$), for stress ($P<0.0109$), and for the interaction between stress and humidity

Table I-5: **Probability values for rate of bud flush of terminal and top three lateral buds, and for overall seedlings from the beginning of bud flush.**

	Terminal		Lateral		Seedling	
	Exp. 1	**Exp. 2**	**Exp. 1**	**Exp. 2**	**Exp. 1**	**Exp. 2**
Humidity	0.2705	0.0051	0.1160	0.0020	0.0001	0.0001
Stress	0.0533	0.0669	0.6840	0.0109	0.0075	0.0001
Stress*Hum	0.2705	0.3779	0.9188	0.0001	0.4302	0.4192
Contrast						
Unstressed						
80 vs 25 & 50%		0.0294		0.0001		
25 vs 50%		0.0128		0.2529		
Stressed						
80 vs 25 & 50%		0.4546		0.2710		
25 vs 50%		0.1987		0.0607		

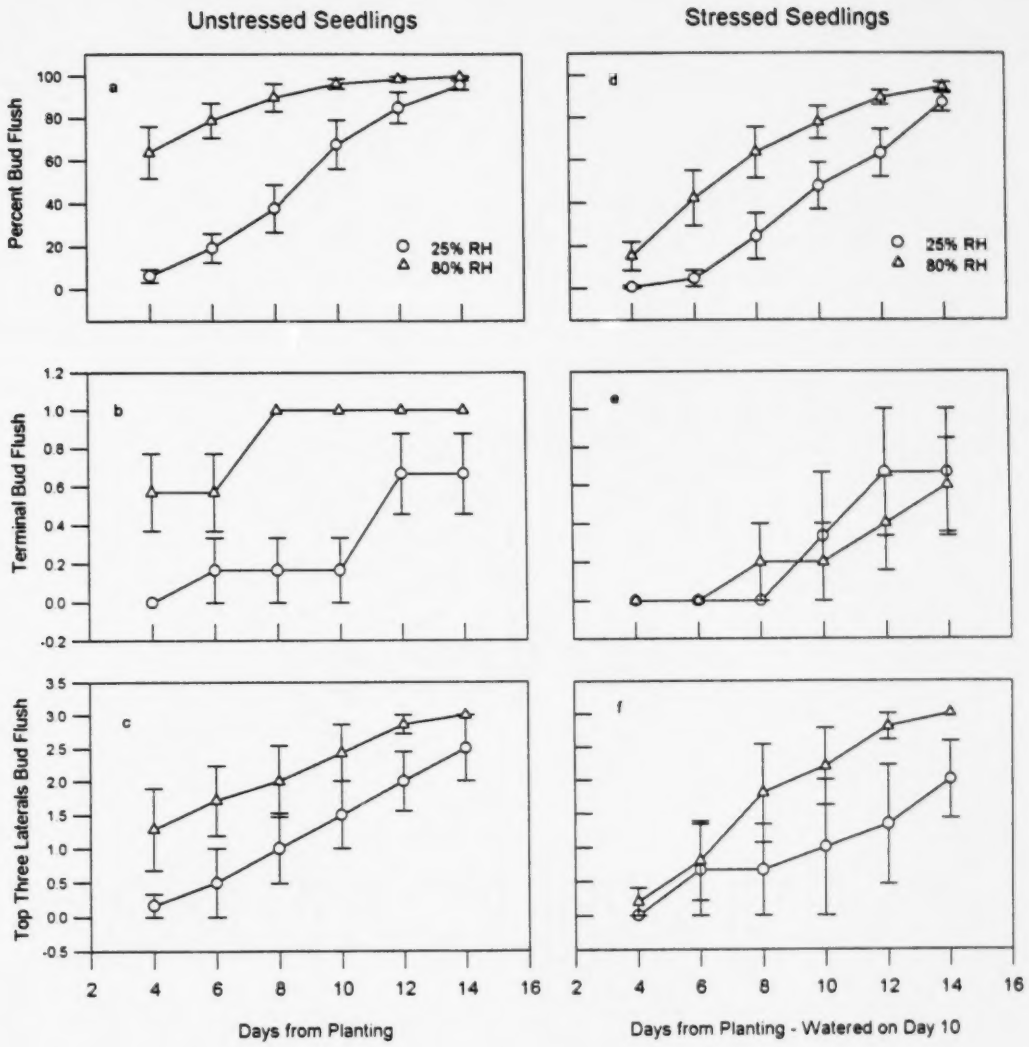

Fig. I-5 (a to f) Bud flush (%), terminal bud break, and number of top three lateral buds flushed over 14 days in Experiment 1. Data not available for 50% stressed and unstressed seedlings.

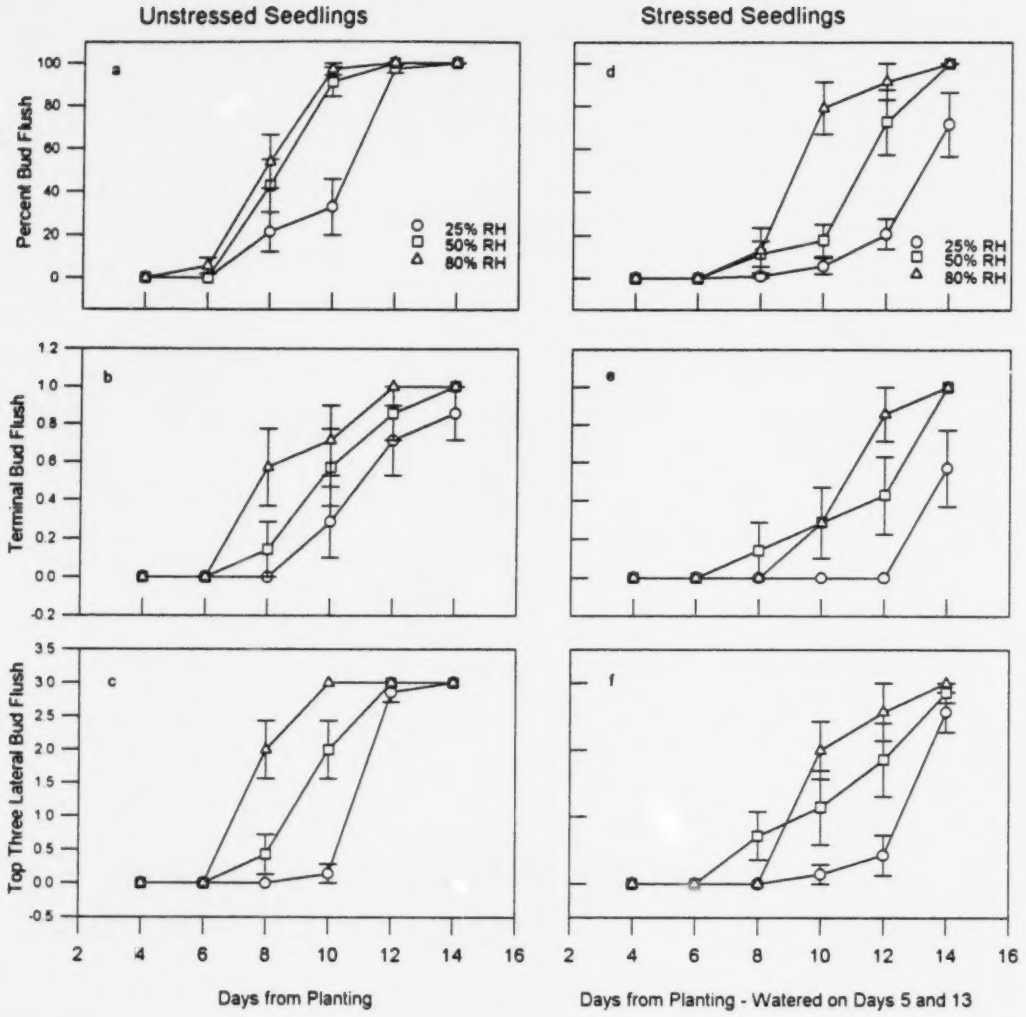

Fig. I-6 (a to f) Percent of bud flush, terminal bud break, and number of the top three lateral buds flushed for unstressed and stressed seedlings over 14 days in Experiment 2.

($P<0.0001$) (Table I-5). For unstressed seedlings, the lateral bud flush was faster ($P<0.0001$) in the 80% treatment over the 25 and 50% treatments, but there was no difference between the 25 and 50% groups (Table I-5, Figs. I-6c and I-6f). There was no significant difference in lateral bud flush among stressed seedlings (Table I-5).

Discussion

These experiments show quite clearly that humidity has a very important role in the performance of white spruce seedlings. White spruce seedlings grown under 80% humidity had higher levels of stomatal conductance than those grown under lower humidity treatments. The difference was substantial; at 80% humidity, there was a 2.3 fold increase in stomatal conductance in stressed plants, and a 200% increase in unstressed plants, over the 50 and 25% treatment groups. In the second experiment, well watered seedlings under 80% humidity had a 390% increase in stomatal conductance above the those in the other two humidity treatments. Among stressed plants, the rate of stomatal conductance was 230% higher at 80% humidity, similar to Experiment 1. This agrees with a study by Livingston and Black (1987), who found that high vapour pressure differences reduce stomatal conductance even when soil moisture is not limiting. Photosynthesis followed a similar pattern to stomatal conductance, with increases of 145 to 190% in stressed seedlings, and an average increase of 130% in well watered plants at 80% humidity over those at 50% humidity in both experiments. This concurs with Bunce (1984), who found that net assimilation decreases with increasing absolute humidity difference.

These results indicate that high humidity surrounding the plant has a large positive effect on the seedling's ability to photosynthesize, even under stressed conditions. The dramatic improvement in stomatal conductance and photosynthesis suggests that the humidity level surrounding the leaf is an important factor in maintaining guard cell turgor,

and directly affects the seedling's ability to photosynthesize while maintaining adequate shoot xylem water potentials.

There appears to be a threshold where humidity has an effect on the stomatal conductance of plants experiencing drought stress. In both experiments, high rates of stomatal conductance occurred only at 80% humidity. Plants in the 25 and 50% humidity treatments had similar low levels of stomatal conductance and net assimilation. This indicates that white spruce stomata respond directly to humidity, regardless of water status, and concurs with Johnson and Ferrell (1983), who suggest that stomatal response to vapour pressure deficits is a "direct physical response to changes in supply of, and demand for, transpirational water". Cowan (1977) suggested that low humidity increases the evaporative demand on the leaf epidermis and guard cell complex, resulting in lower guard cell turgor. Since guard cells require full turgor to remain open (Hsaio 1973), this provides a simple mechanism for protecting leaf water status. Several studies agree with this direct mechanism theory, which "involves both a high rate of transpiration directly from and around the stomatal complex and a substantial hydraulic resistance between the xylem tissue and the stomatal complex" (Sandford and Jarvis 1986). Grace et al. (1974) found that there was no difference in total leaf water potential of sitka spruce under varying absolute humidity differences. Likely, the guard cells respond quickly to changes in evaporative demand, thereby closing before leaf water status was affected. The growth chamber experiments indicate that under conditions of limited soil moisture, the relative humidity of the air surrounding the seedling must be greater than 50% for stomata to remain open.

Transpiration levels in the first experiment were significantly higher under 80% humidity in both stressed and unstressed seedlings. For well watered seedlings, there was also a significant increase in transpiration between 25 and 50% humidity, while drought stressed seedlings performed similarly at these humidity levels. This was the inverse of what was expected, since the lower evaporative demand at 80% humidity should have resulted in lower rates of transpirational water loss. This result was probably due to the method used in the first experiment for taking these measurements with the IRGA. The air in the cuvette was dried to 7% RH, exposing the open stomata to very dry air, so that the results indicate more about the stomatal condition of the seedling and the dry air in the cuvette than actual transpirational water losses under the three humidity treatments. To compensate for this problem, in the second experiment the air in the cuvette was maintained at the ambient humidity conditions under which the seedlings were growing. For well watered seedlings, transpiration levels were highest under 25% humidity, while plants under the 50 and 80% humidity treatments showed similar low levels of transpiration. Seedlings experiencing water stress had the same rates of transpiration, regardless of the ambient humidity level around the leaf. At the same time, under 80% humidity, these seedlings had significantly higher rates of stomatal conductance and net assimilation. This indicates that higher humidity allowed the stomata to remain open and photosynthesis to continue, while preserving the water status of the plant.

Leader length was unaffected by either stress or humidity treatments, and therefore free growth did not occur under high humidity, contrary to expectations. The leaf internodal length of unstressed seedlings under 80% humidity was shorter (35.9 mm ±3.7)

than those at 50% humidity (48.3 mm ±2.5) or at 25% humidity (43.8 mm ±2.8). This preliminary study indicates that high humidity levels result in a decrease in leaf internodal length while leaf morphology remains unchanged. The environment in the year prior to shoot extension has a greater influence on shoot length than that during the period of extension (Pollard and Logan 1977; Ford 1980). A study should be done on the effect of humidity on the number of bud primordia formed in the first season after planting, and on the subsequent leader growth in the following year.

Rates of bud flush were affected by humidity, with seedlings in the 80% humidity treatment flushing 2 to 6 days earlier than those under 25% humidity. This may have importance for growth in the following year, but did not influence leader growth in the first season.

Burdett (1990) suggests that seasonal changes in shoot growth affect the availability of photoassimilates for root growth, and that shoot and root growth do not occur at the same time. Grossnickle and Heikurinen (1989) found that field planted white spruce seedlings produced approximately twice as much new shoot material as new roots. It has been shown that current photosynthate is necessary for new root growth, but that photosynthetic activity itself is not a sufficient condition to cause root growth (Burdett 1990). This appears to be the case in this study, since seedlings under high humidity had photosynthetic rates 100 to 200% higher than seedlings under 25% and 50% humidity, yet there were no significant differences in the number of new roots produced. It is likely that given the conditions of the growth chambers, root growth under all treatments was adequate for white spruce seedlings coming out of dormancy, and that resources were

allocated to bud flush, shoot diameter growth, and carbohydrate storage. This will probably be followed by added root growth in the summer (Grossnickle pers. comm. 1993). Spring outplanting causes a delay in the normal flush period of root activity that coincides with bud flush, and root activity is not resumed until the summer (Mullin 1963). Following transplanting, if the physiological nature of white spruce seedlings puts shoot growth at a higher priority than root growth, then creating higher humidity conditions around the newly planted seedlings becomes more important. High humidity may allow the seedlings to photosynthesize and to survive during initial establishment, until they are physiologically ready to grow new roots.

Root tip water potentials of seedlings under 25% humidity were similar between the unstressed and the stressed plants, and this similarity was likely due to the stomatal condition of the seedlings. Since stomatal conductance was low under 25% humidity, the seedling's ability to uptake water through the roots was reduced, as was the amount of water lost through transpiration. While closing of the stomata helps the seedling to maintain overall water status, it reduces the driving force for moving water through the plant. Well watered seedlings under 80% humidity had less negative root water potentials, indicating that the stomata were open and water was being drawn through the plant. Under stressed conditions, seedlings at 80% humidity had more negative root water potentials than seedlings at 25% humidity. Since these root water potentials were fairly constant throughout the experiment, despite progressively dryer soil conditions, it suggests that some osmotic adjustment may have occurred in the root tips. By

osmotically lowering the root water potential, the seedling is able to draw more water out of the soil under low soil moisture conditions.

Increasing the humidity around the seedling is beneficial in reducing water stress from excessive transpiration, and allowing photosynthesis to continue. White spruce is adapted to growing in the understory in the boreal mixedwoods. Establishment of white spruce seedlings in very exposed sites is unreliable, as they are planted under environmental and microsite conditions unlike those to which white spruce is adapted. Maintaining proper seedling water balance after outplanting on a reforestation site is important for photosynthesis and subsequent seedling growth (Grossnickle 1988). Silvicultural techniques which promote higher humidity levels on plantation sites could improve white spruce seedling performance and survival during the early establishment phase. A vegetation canopy slows wind speed and tends to elevate relative humidity over most of the day (Oke 1978). The challenge to silviculturalists will be to find the best balance between retaining canopy to maintain high humidity around seedlings, but yet provide sufficient light for acceptable levels of photosynthesis. Partial canopies of overstory trees or companion shrubs and herbs may provide this balance.

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Chapter 2

Effect of a Clearcut, Partial Cut, and a Regenerated Aspen Stand on the Relative Humidity and Microsite Environment Surrounding White Spruce Seedlings

Introduction:

The successful establishment of white spruce (*Picea glauca* (Moench) Voss) depends partially on the physiological status of the seedling at the time of planting, and partially on the environmental conditions of the planting site. "Environmental conditions control physiological processes in plants, and thus their rates of growth" (Margolis and Brand 1990). Microsite conditions of air temperature, light levels, and soil nutrient content, temperature, moisture, and pH have been studied in relation to white spruce seedlings (Burdett 1990). Humidity is an important environmental condition of the planting site, yet little research has been directed towards examining humidity levels in the field, and its effect on the physiological status of the seedling.

Since transpiration is driven by the evaporative demand on the seedling, humidity may have an important influence, particularly on seedling water status. High wind speeds and high temperatures increase evaporation; as air nears the saturation point for water vapour, it becomes less effective at drawing water out of the plant. Clearcut sites create high evaporative demands on seedlings, since there is no shade to reduce light and heat, and little surrounding vegetation or other structures to reduce wind speeds (Burdett 1990), or to augment humidity levels through transpiration and trapping of water vapour under the canopy. An understory environment is less variable than a clearcut because the

air under the canopy is less turbulent. Reduced wind speeds allow heat and humidity to diffuse more slowly into the drier air above the canopy.

White spruce is a shade tolerent species, and some problems with plantation performance can be attributed to the natural ecology of the species and the successional patterns of the planting site (Brand and Penner 1990). In the past, aspen was not commercially valuable, and was often left standing on the site following the harvesting of spruce. Shading by residual aspen prevented the invasion of grasses, and restocking of these areas by white spruce was frequently successful (Johnson and Gorman 1977). Forestry practices and silvicultural systems that force relatively pure white spruce stands on mixwood areas are not appropriate to the ecology of the mixedwood site (Lieffers and Beck 1994).

On clearcut sites, extremes of temperature and light expand the range of conditions to which the seedling must adapt in order to survive and grow. Water stress in outplanted white spruce seedlings is typical, even when soil water is plentiful (Burdett 1990; Colombo and Teng 1992), and is usually associated with elevated atmospheric evaporative demand and/or low soil water availability (Bernier 1993). High evaporative demands over clearcut sites and a dependence on rainfall for an immediate water supply contributes to the problem of seedling water stress. Factors affecting plant water status immediately after planting have a decisive influence on establishment success (Burdett 1990). Methods to promote the rapid development of the roots have been suggested to reduce the severity of water stress, but much depends on the physical condition of the stock and the environmental conditions of the site (Burdett 1990). Another approach to reducing water

stress in new transplants is to reduce the evaporative demands on the foliage of the seedling. Increasing the humidity around the seedling should help to alleviate the extent and duration of water stress during drought and following initial planting.

The purpose of this field study was to determine if the relative humidity level under a canopy of young aspen is different than that over a clearcut, and to determine if an aspen stand that has regenerated on a cutblock can provide suitable conditions for white spruce seedling growth. In this experiment, microsite conditions of soil temperature, soil moisture, absolute humidity difference between the leaf and air, and photosynthetically active radiation (PAR) levels at seedling height were examined in a seven year old aspen stand regenerating from a clearcut. The treatments were the uncut aspen, plots with half the aspen removed, and clearcuts. White spruce seedlings were planted to determine the effect of each treatment on seedling physiological parameters and water relations.

Methods:

The field sites were located at Whitecourt, Alberta (Twp. 58 Rge. 14 W. 5 Mer., sections 27 and 34), in an aspen/white spruce mixedwood which was clearcut in 1987 and left to natural regeneration until this study (1993). Three field sites were chosen for similarity in height, density, and diameter at breast height (dbh) of aspen, and were located half a kilometer apart. The three site treatments were 1) no aspen removed, 2) a parial canopy with 50% of the aspen cut to ground level, and 3) a clearcut. The plots were

marked out in 12 meter diameter circles, with a buffer zone of 5 meters between each circle, and then cut with a Stihl F5 280 K brushcutter as required. For the partial canopy plots, aspen saplings were cut down in a zigzag pattern to reduce the possibility of wind channels through the plots. The aspen saplings were approximately 3 meters high, so that the circles were four times as wide as the height of the surrounding vegetation. This removes edge effect, and the centre of the circle approximates the microclimate of a larger area (R. Rothwell pers. comm. 1993). The treatments were replicated at each of the three sites four times in a random block design, with each set of replicates grouped together to form the blocking pattern.

The dbh and density of the aspen on each plot was determined. Density was estimated using the point-centered quarter method (Cottam and Curtis 1956). In each plot, three random points were selected. At each point, the closest tree in each of the four quarters around the point was chosen as the sample. The distance of that tree to the point was recorded, along with its dbh. The average of the four distances gives the square root of the mean area per plant. The reciprocal gives the density in plants per meter squared. The dbh was measured using the trees sampled in the density estimates, and averaged for each. Photosynthetically active radiation (PAR) in each treatment plot was measured on August 18 and 19, 1993 using a Sunfleck Ceptometer Model SF-80 (Decagon Devices Inc.). Measurements were taken between noon and 2 pm, with the first and last readings in each plot taken directly above the seedlings, and the remaining eight readings taken at a distance of 1 meter from the edge of the planted area, circling the seedlings. The ceptometer was held at 50 cm above ground for all readings.

Three year old white spruce seedlings were obtained from Pine Ridge Forest Nursery at Smoky Lake, Alberta. Seedlings were fall-lifted 1.5 + 1.5 bareroot stock from a Whitecourt seed source. This means that the seedlings were grown for the first year and a half in the nursery before being transplanted outside for another year and a half, and then lifted in the fall and stored overwinter in a cooler at -2°C. After removal from cold storage, the seedlings were thawed at 4°C for three days prior to planting. Twenty seedlings were planted at the centre of each plot on May 27, 1993. A total of 720 seedlings were planted, with another 30 seedlings sampled for initial size and weight analysis. The seedlings had an initial average shoot height of 22.9 cm, root length of 24.5 cm, stem diameter of 5 mm, shoot weight of 8.9 g, and root weight of 2.4 g. Seedling and environmental measurements were taken on June 3 1993, seven days after planting, and on June 17 (Day 21) and July 27 (Day 61). On July 15 the vegetation immediately surrounding the seedlings was cut back, and the plots were re-cut with a weedeater to keep the grasses and aspen sprouts down. The following spring (May 27, 1994), the percentage of flushed buds was recorded for five seedlings per plot, and averaged.

Site and physiological measurements were taken on each sampling day. Site measurements consisted of air temperature and relative humidity at seedling height using a Digital Humidity/Temperature Meter 4465 CF (Extech Instruments). Humidity readings were corrected using an equation derived from calibrating the Digital Humidity Meter with a Bendix Psychron Model 566 psychrometer (wet-dry bulb). Soil temperature was measured from a copper-constantan thermocouple junction inserted in the soil to a depth of 15 cm. An ice-point junction attached to a multimeter provided a millivolt reading

which was multiplied by 25.2 to calculate soil temperature. One soil core to a depth of 20 cm was taken from each plot using a standard soil corer, with the duff layer removed before the core was placed in a plastic bag for return to the lab. Each soil core was weighed wet, and then dried for 48 hours at 105°C and reweighed. Soil moisture content was expressed on an oven dry-weight.

For the physiological measurements, one seedling from each replicate of each treatment at each site (36 seedlings) was randomly selected on each sampling date. An LCA-2 Infrared Gas Analyzer (IRGA) equipped with a conifer cuvette was used to collect data on net assimilation, transpiration, and stomatal conductance to CO_2. Air flow rate was set at 8 ml/s, and a quartz halogen lamp was positioned to boost light in the cuvette to 1000 $\mu mol\ m^{-2}s^{-1}$. A high speed fan built into the cuvette created turbulence, reducing the boundary layer resistance around the leaves. Ambient air was drawn in from a 4 m high tower, and passed through a silica gel desiccant (anhydrous $CaSO_4$, 6 to 16 mesh) before entering the cuvette.

A lateral branch midway along the seedling was selected for gas exchange measurements. To lessen the variability of the measurements, attempts were made to select branches uniform in size and position on the seedling. The leaves were stripped from the branch at the point of contact with the cuvette to ensure a better seal. Care was taken to avoid tearing the outer bark of the branch. After measurement, the branch was clipped and sealed in a plastic bag for leaf area analysis. The air temperature inside the cuvette was used as an estimate of leaf temperature for the gas exchange measurements. The value for the boundary layer resistance was from a previous study on 3 year old black

spruce seedlings (S.E. Macdonald, pers. comm. 1993). The atmospheric pressure was obtained from Environment Canada's Climate Services, as recorded at noon on each measurement day at the Whitecourt station.

In the lab, the branch used for IRGA analysis was dipped in liquid nitrogen for 10 seconds to ease the removal of the leaves. The leaf area of each sample was then determined with an LI 3100 Leaf Area Meter (Lambda Instruments Corp.). Three measurements of the projected leaf area were taken and averaged, then multiplied by 2 to estimate the total leaf area. All recorded measurements from the IRGA were run through a series of calculations to obtain the gas exchange parameters (von Caemmerer and Farquhar 1981).

The leaf temperature was measured using a thermocouple junction with copper-constantan wire 0.12 mm in diameter with one end formed into a 3 mm loop. The loop was slipped over the leaf and twisted slightly to improve wire contact with the leaf. The lead wires were shaded from the sun to prevent heating of wires. An ice-point junction attached to a multimeter provided a voltage reading which was then multiplied by 25.2 to calculate leaf temperature. This was recorded for five leaves per plant and averaged.

The evaporative demand on the seedling is the absolute humidity difference (AHD) between the needle and the air, and was calculated for each plot using air temperature, needle temperature, and relative humidity around the seedling. The following formulas were used to calculate absolute humidity difference:

$\ln e_s = 21.832 - (5.3475 \times 10^{3} / \text{Temp K}^\circ)$

$e = (RH/100) \times e_s$

$Pv = 217 \times e / \text{Temp K}^\circ$

$VPD = e_s - e$

$AHD = Pv\ (leaf) - Pv\ (air)$

where e_s is the saturation vapour pressure (kPa), e is vapour pressure (kPa), RH is the relative humidity (%), Pv is the absolute humidity ($\mu g\ cm^{-3}$), VPD is the vapour pressure deficit (kPa), and AHD is the absolute humidity difference (Lee 1978).

Shoot xylem water potential was determined by clipping another lateral branch from midway along the seedling. The outer bark and leaves were carefully stripped off the bottom 2 cm of the branch, which was then inserted into a Scholander Pressure Bomb (PMS Instr. Co., U.S.), with the cut end projecting through the rubber stopper. Compressed nitrogen gas was released gradually into the chamber increasing the pressure, and a reading was taken when the xylem sap appeared on the cut surface of the branch. This pressure reading is a good estimate of xylem water potential in the plant (Ritchie and Hinckley 1975). Finally, the seedling was dug up, taking care to preserve the root system, placed in a bag, and taken to the lab for a count of the number of new white roots.

Statistical Analysis:

Analyses of variance were performed using the general linear model (two way ANOVA with interaction, mixed model). Where significant differences occurred, the

contrast testing procedure of SAS (SAS Institute Inc.) was used to test for these differences. The significance level of each comparison test was adjusted to $\alpha' = 0.0127$ for an experiment-wise error rate of $\alpha = 0.05$, according to the Dunn-Sidak method for non-orthogonal planned comparisons (Sokal and Rohlf 1981). Graphing was done using the Means procedure of SAS, incorporated into Sigma Plot (Jandel Scientific Inc.).

Results:

All plots were located on level ground. Average monthly precipitation levels in the Whitecourt area were 98.9 mm (June), 117.8 mm (July), and 103.1 mm (August). Average monthly maximum and minimum temperatures were: 19.3/6.8°C (June), 19.6/8.6°C (July), and 19.5/7.7°C (August). Brush removal of the aspen in the partial canopy plots resulted in a difference ($P<0.0001$) in density from the full canopy plots. Full canopy plots averaged 47,000 (±10,000) stems per hectare, while the partial canopy plots averaged 21,000 (±6000) stems per hectare. The density of the brushed plots was 45% of the uncut plots. There were no differences in density between sites. The diameter at breast height (dbh) of the aspen was similar in both treatments. Average dbh was 16.9 (±1.2) mm for the full canopy, and 17.3 (±1.8) mm for the partial canopy plots. There was a site difference ($P<0.0101$) in dbh, with the aspen in both the full canopy and the partial canopy treatment plots in Site 1 being slightly larger than those in Sites 2 and 3.

Levels of PAR at seedling height were different ($P<0.0001$) between the full canopy and the partial canopy plots, and different ($P<0.0001$) between the full canopy and the clearcut, but not between the partial canopy and the clearcut plots. There was also a site difference ($P<0.0001$) between Site 1 and Sites 2 and 3. Average PAR was 497.3 (±24.6) μmol $m^{-2}s^{-1}$ in the full canopy plots, 667.9 (±28.0) μmol $m^{-2}s^{-1}$ in the partial canopy plots, and 1325 (±67.1) μmol $m^{-2}s^{-1}$ in the clearcuts. This resulted in PAR at seedling height being 38% of full light for the full canopy plots, and 50% of full light for the partial canopy plots.

There was no difference in soil moisture content between treatments or between sites. There was a difference ($P<0.0253$) over time, as expected (Table II-1).

There was a difference ($P<0.0003$) in soil temperature between treatments, and also a difference ($P<0.0005$) between sites. There was no difference in soil temperature between the vegetated treatments, but the full canopy had lower ($P<0.0002$) soil temperatures than the clearcut, as did the partial canopy plots ($P<0.0014$) (Table II-1, Fig. II-1). Soil temperatures averaged 12.4°C (±1.8) in the full canopy plots, 12.6°C (±1.7) in the partial canopy plots, and 13.7°C (±1.8) in the clearcuts, so that there was only a 1°C difference in soil temperature between treatments. There was no difference in soil moisture content between treatments or between sites. There was a difference ($P<0.0253$) over time, as expected (Table II-1).

AHD was different ($P<0.0052$) between treatments (Table II-1). Altering the density of the aspen did not produce a significant difference in AHD between the full canopy and the partial canopy plots, but there was a difference ($P<0.0024$) between the

Table II-1: Probability values for seedling physiological parameters and site conditions.

Source	Net Assimilation	Stomatal Conductance	Transp.	Root Count	Percent Bud Flush	Xylem Water Potential	Soil Moisture	Soil Temp	AHD
Tmt	0.7531	0.8199	0.8065	0.8703	0.0002	0.0839	0.0731	0.0003	0.0052
Site	0.2558	0.1292	0.1624	0.4425	0.0043	0.0187	0.0831	0.0005	0.0001
Day	0.0001	0.0001	0.0001	0.0001	-	0.0001	0.0253	0.0001	0.0001
Tmt*Day	0.9598	0.8987	0.8947	0.9511	-	0.7488	0.7860	0.8692	0.8577
Tmt*Site	0.6290	0.5264	0.6953	0.5128	0.2246	0.5385	0.6952	0.7203	0.6399
Site*Day	0.0957	0.0218	0.0714	0.3781	-	0.0001	0.7190	0.0001	0.0001
Tmt*Site*Day	0.7312	0.6280	0.8509	0.3500	-	0.9583	0.5963	0.8940	0.9669
Contrasts - Treatment Differences									
Tmt 1 vs 2	-	-	-	-	0.2731	-	-	0.5133	0.5940
Tmt 2 vs 3	-	-	-	-	0.0001	-	-	0.0014	0.0111
Tmt 1 vs 3	-	-	-	-	0.0013	-	-	0.0002	0.0024
Contrasts - Site Differences									
Site 1 vs 2						0.0191		0.0506	0.0001
Site 2 vs 3						0.0114		0.0402	0.7866
Site 1 vs 3						0.8451		0.0001	0.0001

Note: **For Contrasts, the P value must be less than 0.0127 to be significant at of $\alpha = 0.05$**
Treatments are: Full Canopy (Tmt 1), Partial Canopy (Tmt 2), and Clearcut (Tmt 3)

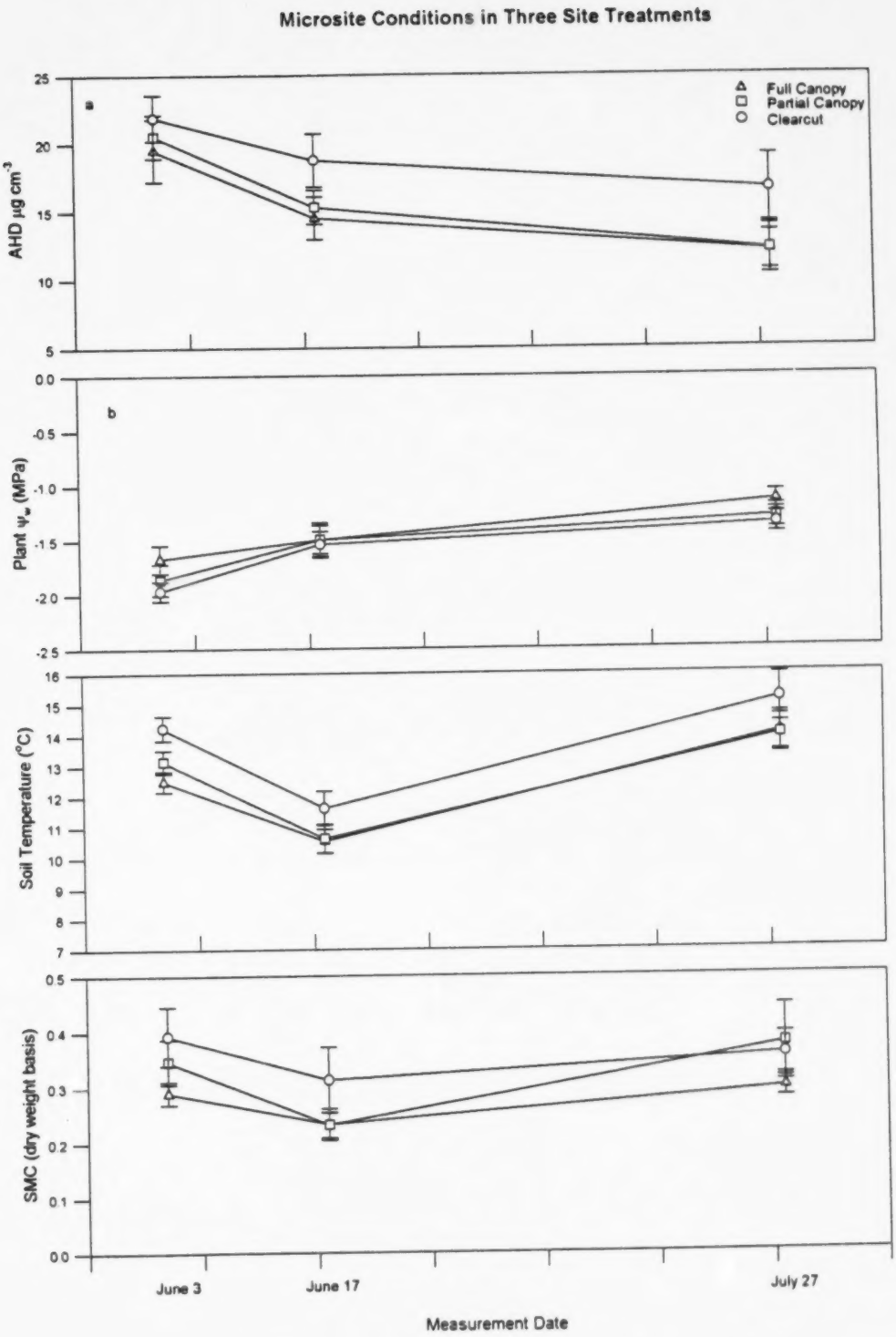

Fig. II-1(a to d) Absolute humidity difference (AHD), soil temperature, soil moisture content, and shoot water potentials. Site treatments are full canopy, partial canopy, and clearcut.

full canopy and the clearcut, and also a difference ($P<0.0111$) between the partial canopy and the clearcut in absolute humidity levels (Table II-1). AHD was highest in the clearcuts for all measurement days. AHD levels in the full canopy and the partial canopy plots were similar, with the levels under the partial canopy being slightly higher than under the full canopy (Fig. II-1). Differences in AHD also occurred between sites ($P<0.0001$) (Table II-1). The difference ($P<0.0001$) between days was as expected, and the interaction ($P<0.0001$) between site by day was due to differences in AHD values between the sites.

There were no significant differences in photosynthesis, stomatal conductance, or xylem water potentials among the seedlings (Table II-1). There was also no significant difference in the number of new roots produced by the seedlings (Table II-1).

The treatments had an effect ($P<0.0002$) on the rate of bud flush in the following spring. While bud flush in the full canopy and the partial canopy plots were the same, in the clearcut it was later than in the partial canopy plots ($P<0.0001$) and the full canopy plots ($P<0.0013$) (Table II-1). There was also an effect of site ($P<0.0043$) on the percentage of bud flush of the seedlings, with Site 3 producing lower levels of bud flush than Sites 1 and 2 (Table II-1, Fig. II-2). Percentage of bud flush on May 27, 1994 was low in the clearcuts (54.7% ±25.1), as compared to the full canopy (82.6% ±8.1) and the partial canopy sites (91.0% ±11.5) (Table II-2; Fig. II-2).

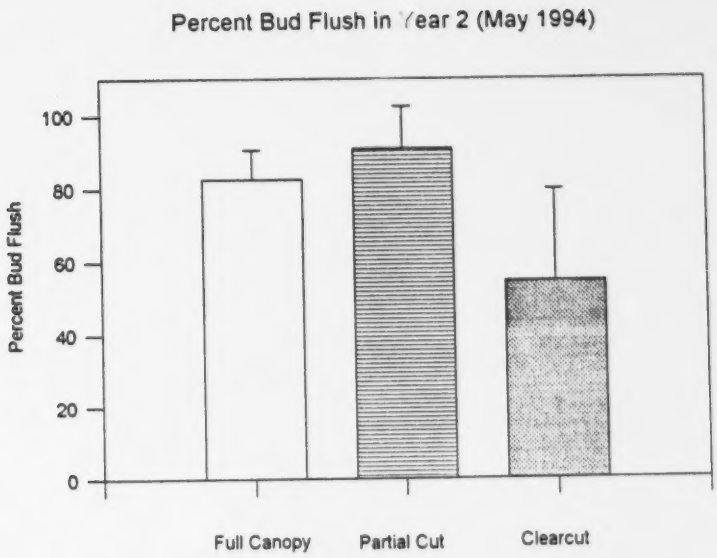

Fig. II-2 Percent bud flush in second year following planting of white spruce seedlings. Site treatments are full canopy, partial canopy, and clearcut.

Table II-2: Means and standard errors for seedling physiological parameters and site conditions.

	Net Assimilation $\mu mol\ m^{-2}s^{-1}$	Stomatal Conductance $mmol\ m^{-2}s^{-1}$	Transp. $mmol\ m^{-2}s^{-1}$	Percent Bud Flush May 1994	Shoot Water Potential MPa	Soil Moisture by Dry Wt.	Soil Temp °C	AHD $\mu g\ cm^{-3}$
Full Canopy								
Day 7	0.45 (±0.08)	7.52 (±1.12)	0.35 (±0.13)		-1.67 (±0.13)	0.29 (±0.02)	12.49 (±1.760	19.53 (±2.28)
Day 21	1.45 (±0.46)	14.19 (±2.44)	0.62(±0.09)		-1.49(±0.13)	0.23 (±0.03)	10.54 (±0.39)	14.51 (±1.57)
Day 61	8.29 (±2.55)	108.89 (±37.17)	5.16 (±1.52)		-1.15 (±0.08)	0.30 (±0.02)	14.05 (±0.63)	12.02 (±1.41)
Total				54.7 (±25.10)	-1.44 (±0.26)	0.27 (±0.04)	12.36 (±1.76)	15.35 (±3.83)
Partial Canopy								
Day 7	0.32 (±0.14)	6.95 (± 1.20)	0.34 (±0.05)		-1.86 (±0.15)	0.35 (±0.04)	13.15 (±0.36)	20.56 (±1.59)
Day 21	0.58 (±0.39)	17.28 (±2.94)	0.78 (±0.13)		-1.49 (±0.15)	0.23 (±0.02)	10.63 (±0.47)	15.32 (±1.26)
Day 61	5.81 (±1.52)	80.33 (±14.00)	3.93 (±0.63)		-1.30 (±0.11)	0.38 (±0.07)	13.96 (±0.61)	12.10 (±1.81)
Total				91.1 (±11.50)	-1.55 (±0.28)	0.32 (±0.08)	12.58 (±1.74)	15.99 (±4.27)
Clearcut								
Day 7	0.44 (±0.17)	9.82 (±2.07)	0.47 (±0.09)		-1.97 (±0.09)	0.39 (±0.05)	14.24 (±0.39)	21.92 (±1.69)
Day 21	0.63 (±0.38)	16.99 (±3.16)	0.79 (±0.10)		-1.54 (±0.12)	0.31 (±0.06)	11.61 (±0.56)	18.78 (±1.95)
Day 61	8.32 (±5.10)	93.03 (±34.26)	4.70 (±1.43)		-1.36 (±0.09)	0.36 (±0.04)	15.14 (±0.79)	16.62 (±2.50)
Total				82.6 (±8.10)	-1.62 (±0.31)	0.35 (±0.04)	13.66 (±1.83)	19.12 (±2.67)

Discussion:

This experiment showed that there was a difference in AHD in relation to vegetation cover. AHD levels across the clearcut sites were significantly higher than under an aspen canopy. Thinning the aspen canopy had no effect on AHD as compared to the fully forested stand, and both had similar and lower levels of AHD than the clearcuts. Measurements of humidity, leaf temperature, and air temperature were taken between 9 am and 5 pm on each measurement day, and may reflect mid-day AHD values only. Since relative humidity is usually highest at dawn and dusk, these times should be included in the estimate of AHD. Further study is needed to determine the total diurnal and total seasonal AHD in these plots. In this study, average AHD was 15.4 (±3.8) $\mu g\ cm^{-3}$ under the full canopy, 16.0 (±4.3) $\mu g\ cm^{-3}$ under the partial canopy, and 19.1 (±2.7) $\mu g\ cm^{-3}$ in the clearcuts. This indicates that only a light canopy of aspen is required to improve humidity around the seedling. Since PAR levels of 39 to 50% of full light occurred in the vegetated treatments, adequate light levels were retained for full photosynthesis in white spruce seedlings. Soil moisture levels were similar between treatments, though soil temperatures were slightly lower in the vegetated sites. The difference in AHD in relation to vegetation cover reflects a difference in the evaporative demand on the seedling. Improving humidity levels and reducing vegetative competition may outweigh the disadvantage of slightly lower soil temperatures.

There was little impact of the treatments on the physiology of the seedlings. After planting, there was little rain for six weeks, followed by rainy conditions for another six

weeks. The poor, or perhaps typical field conditions in the summer of 1993 prevented the seedlings from performing well under any of the treatments. Rates of net assimilation and stomatal conductance were uniformly low, and are likely associated with the hot, dry conditions. Seedling water status was similar under all treatments. It is possible that differences in seedling physiology between the site treatments were not detected, since measurements were taken at only three points throughout the summer. A closer monitoring of the seedlings during the first 20 days following planting may have given a clearer indication of any differences in the treatments on seedling physiology.

In the winter, the *in situ* oblation of the snowpack and loss to blowing snow has the potential to increase the mortality of seedlings in clearcuts, either by reducing spring soil moisture or from the lack of protection that snowcover of reasonable depth provides (Bernier 1993). Studies in a mixed lodgepole pine (*Pinus contorta* Dougl.) and red fir forest have shown that snow evaporation doubles between 0.5H and 8H openings (where H is the height of the surrounding trees), and that small 1H openings delay melt and provide as much protection against snow evaporation as a full forest (Bernier and Swanson 1993; West 1962). This is another benefit to planting under a canopy, and may help to reduce seedling water stress in the year following planting.

Interesting results occurred with the percentage of bud flush in the spring following planting, and further suggests that differences in seedling phsyiology among treatments occurred, although they weren't detected on the three measurement days. Percentage of bud flush in the clearcuts was low (54.7% ±25.1), as compared to the full canopy sites (82.6% ±8.1) and the partial canopy sites (91.0% ±11.5). Clearly, the

seedlings under an aspen canopy flushed earlier than those in the clearcut, and this may indicate a healthy physiological status in these seedlings. Lieffers (1987) suggests that the timing of bud flush in black spruce and tamarack (*Larix laricina* (Du Roi) K. Koch) may be related to the number of leaf primordia, and that the scales of larger buds cannot contain the expanding tissues as long as the scales of smaller buds. The more rapid bud flush under the canopy may indicate that there are more leaf primordia in the buds, and reflect the environmental conditions from the previous year (Lieffers 1987; Pollard and Logan 1977). This suggests that total seasonal photosynthesis was greater under an aspen canopy than in the clearcuts. If microsite conditions on the vegetated sites significantly increases the number of leaf primordia (as may be indicated by the early bud flush), then second year field growth and survival may show further differences between these treatments. Seedling water status may have been affected by higher spring soil moisture levels and improved winter environmental conditions in vegetated sites. Further study of survival rates of the seedlings was not done in this experiment, but the low percentage of bud flush in the clearcuts may indicate seedling losses. Early bud flush may allow the seedlings to absorb more of the spring light and may improve subsequent growth. A study of the effect of these treatments on the second year's growth would provide more information about the physiology and survival of white spruce seedlings planted under a canopy.

The major concern of silviculturalists with vegetation on the planting site involves the amount of photosynthetically active radiation (PAR) reaching the seedling, soil temperature and moisture levels, and vegetative competition for nutrient and water

resources (Burdett 1990). This study shows that in a young aspen stand, PAR levels at seedling height in mid-August were within the 40-45% of full light required for maximum photosynthesis of white spruce seedlings. Soil moisure content was unaffected by treatment. A young aspen stand could provide adequate conditions for white spruce seedling growth, while reducing the silvicultural problems associated with vegetation competition from shade intolerent species. Studies have shown that a canopy can reduce vegetative competition, particularly of *Calamagrostis canadensis*, which can outcompete or snow press newly planted seedlings (Lieffers and Stadt 1994).

The controlled growth chamber experiments showed that humidity has a large effect on the net assimilation and stomatal conductance of seedlings, and promotes early bud flush. Silvicultural treatments which take advantage of the influence of humidity on white spruce seedlings should result in improved seedling establishment and survival.

This study indicates that there is some potential for improved white spruce establishment if silvicultural treatments are aimed at working within the natural regeneration system of the mixedwood forest. Following a clearcut, aspen will rapidly invade the cutover, and if it is not too dense will create suitable conditions for understory growth. Since white spruce seedlings are sensitive to large AHD and tolerent of shade, early establishment and growth would likely be improved under a canopy. At some point, the aspen could be harvested, releasing the white spruce. This may reduce costs of reforestation, and reduce the need for herbicides on white spruce plantations.

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General Discussion

The growth chamber experiments showed that humidity influences the photosynthesis and stomatal conductance of white spruce seedlings to a great extent, even under stressed conditions. Rates of bud flush were also faster under higher humidity levels, indicating good seedling physiology and water status. Given these results, humidity should be considered along with light, air temperature, and soil temperature as an important environmental influence on the planting site, and on the growth of transplanted seedlings.

The field study demonstrated that humidity conditions around the seedling can be altered by vegetative cover. AHD over the clearcut was 19.1 (±2.7) $\mu g\ cm^{-3}$, similar to the AHD between the leaf and the air at 25% humidity. Under an aspen canopy, AHD dropped to 15.4 (±3.8) $\mu g\ cm^{-3}$, similar to AHD at 50% relative humidity. The results of the growth chamber study suggest that there may be a threshold where humidity has an affect on stomatal conductance of plants under stress. In white spruce seedlings, stomatal conductance increases above 50% RH. During the field season, hot dry conditions resulted in uniformly low levels of photosynthesis and stomatal conductance in white spruce seedlings. It is possible that humidity levels under the canopy were still not high enough to improve seedling response to transplanting when conditions are very dry. While the physiological status of the seedlings during the first season did not appear to be different between the treatments, the rate of survival of seedlings in the second season was

better under a canopy. The amount of bud flush in the spring following planting was almost doubled under a canopy as compared to the clearcut. Snow retention during winter and spring, and shading in the summer, may also contribute to better water status of seedlings under a canopy.

The field study did not include measurement of diurnal patterns of humidity. It is likely that actual humidity levels were higher, or persisted for longer periods, than was recorded in this study. A study of diurnal humidity patterns and second year growth would provide better insight into the effect of a canopy on white spruce seedling establishment. Other silvicultural treatments which could improve humidity around the seedling should be considered.

Root growth of seedlings were unaffected by site treatments in the field study, and unaffected by either humidity or stress in the growth chamber experiment. Even under optimum conditions in the growth chamber, seedlings failed to produce more roots than seedlings under stressed conditions. It is likely that transplanting interrupts normal root activity, which is not resumed until after bud flush. The effect of transplant shock and the natural cycle of root growth in white spruce seedlings should be examined further. If white spruce seedlings are physiologically unable to develop new roots quickly, then reducing the evaporative demand on the foliage is an important means of reducing water stress.

The challenge to silviculturalists will be to find the best balance between retaining canopy to maintain high humidity around the seedlings while providing 45% of full light required for seedling growth. In this study, both the full canopy and the partial canopy

provided adequate light while slightly improving humidity levels. Diurnal humidity levels coupled with added humidity from herbs and grasses in the understory would likely produce a higher humidity level than those reported in this study. Rates of bud flush in the second field season indicate better seedling physiological status and possibly more leaf primordia in the bud. These are influenced by environmental conditions of the previous year. This suggests that the treatments would have affected seedling physiological status, despite low responses in the first growing season.

Growth chamber conditions were considerably warmer than field conditions, having a 22°C day/18°C night temperature regime as opposed to average day temperatures of 19.5°C and night temperatures of 7.7°C in the field. Water potentials of seedlings in the field were similar to those in the growth chamber. A poorer physiological response would be expected under cooler and more extreme day/night temperature differences. The effect of humidity levels on chilling stress (above 4°C) should be examined to further assess its influence on white spruce physiology. Diurnal level of AHD would necessarily incorporate the almost 12° difference between day and night temperatures.

The aspen stand in this study regenerated naturally on a clearcut site, and created mid-day AHD similar to that under 50% relative humidity in a controlled environment. The light levels were adequate for potential full photosynthesis in the seedlings. Although a vegetation sample was not taken, the sites were abundant with strawberry, raspberry, blueberry, bearberry, and various other herbs and flowers. A silvicultural system which incorporates natural mixedwood regeneration would also improve the biodiversity on the planting site. Problems associated with soil compaction from roadways and heavy

equipment could be reduced, particularly if the area is harvested when underground root systems are least likely to be damaged. In a mixedwood ecosystem, mixtures of aspen and white spruce are more productive than pure stands. Since aspen is now commercially in demand, a silvicultural system which incorporates mixedwood ecology should also be a more economical system. It is likely that improving the humidity around white spruce seedlings with vegetation on the site will result in increased survival and better rates of growth over seedlings planted on clearcut sites.